SYSTEMATIC STUDIES IN NEOTROPICAL 'CAESALPINA L.' (LEGUMINOSAE: CAESALPINIOIDEAE), INCLUDING A REVISION OF THE 'POINCHIANELLA-ERYTHROSTEMON' GROUP

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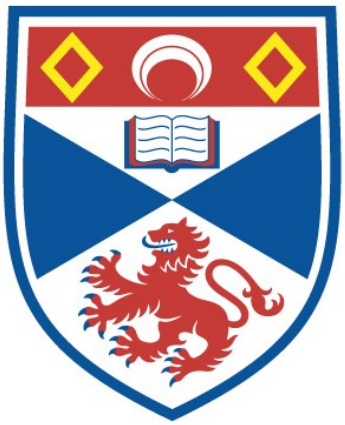
at the
University of St Andrews



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Systematic Studies in Neotropical *Caesalpinia* L. (Leguminosae: Caesalpinioideae), including a revision of the *Poincianella-Erythrostemon* group

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Branchlet from a mature tree of *Caesalpinia pluviosa* var. *sanfranciscana* in Bahia, Brazil, the two leaflet types have resulted in much taxonomic confusion; this is a phenomenon typical of several species in the genus.

To Richard, who survived to

see this thesis

DECLARATION

I, Gwilym Peter Lewis, hereby certify that this thesis has been composed by myself, that it is a record of my own work, and that it has not been accepted in partial or complete fulfilment of any other degree or professional qualification.

Gwilym Lewis

July 1994

STATEMENT

I was admitted to the Faculty of Science of the University of St. Andrews under the Ordinance General No. 12 on October 1st 1986 and as a part-time candidate for the degree of PhD. on October 1st 1987.

Gwilym Lewis

July 1994

CERTIFICATE

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate to the Degree of PhD.

Signature of Supervisor

P.E. Gibbs

July 1994

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ABSTRACT

The pantropical genus *Caesalpinia sensu lato* contains about 120 to 130 species, of which 70 to 75% are neotropical. The genus belongs in the *Caesalpinia* group (Caesalpinioideae: Caesalpinieae) of Polhill and Raven (1981). A morphological cladistic analysis of the *Caesalpinia* group demonstrates that the traditional circumscription of the genus *Caesalpinia* is polyphyletic: some species are more closely related to other genera in the group than to each other. The *Poincianella* and *Erythrostemon* elements of *Caesalpinia sensu lato*, selected for more detailed study, have been united and the resulting, strictly neotropical group, has been expanded to include several South American taxa previously placed in other infrageneric groups of *Caesalpinia sensu lato*. The *Poincianella-Erythrostemon* group has been revised and 56 taxa in 47 species are currently recognised. These have a geographical range from south eastern U.S.A. to southern Chile and most species have a predilection for semi arid areas. A key to species identification, full descriptions and specimen citations are provided; most species are illustrated and all are mapped. One new species, *Caesalpinia coccinea*, discovered during this research, has already been published (Lewis and Contreras, 1994). Eight other new taxa and two new combinations presented here are to be effectively published in a future volume of Kew Bulletin. Sections on morphology, seed chemistry, biogeography and floral biology discuss the relationships between the *Poincianella-Erythrostemon* group and other infrageneric groups of *Caesalpinia s.l.* A survey of floral secretory structures in *Caesalpinia sensu lato* is presented in Appendix 1 and an account of the sexual systems of two species of the *Poincianella-Erythrostemon* group in Appendix 2.

INTRODUCTION

Prior to commencement of this thesis I had concentrated my taxonomic studies on genera in the *Papilionoideae* and *Mimosoideae* subfamilies of the large, diverse family Leguminosae. I considered it desirable to extend my research to the third subfamily *Caesalpinioideae*, so broadening my understanding of the family as a whole at the same time as delving into some of the complexities of the more basal groups within it.

In the mid 1980's it became apparent to me that *Caesalpinia sens. lat.* was a taxonomically and nomenclaturally problematical genus in need of detailed study and revision. I had already encountered difficulty in naming specimens collected in Brazil and the lack of any monographic account for neotropical species suggested the presence of an unacceptable proliferation of names. Some species with a wide geographical range had sufferered name changes at political boundaries - these additional names were introduced by regional Flora writers constrained and blinkered by the political limits of each region. Some species of *Caesalpinia* display a high degree of phenotypic plasticity, especially in foliage; leaflet size, shape and indumentum can all vary greatly within a small population of a single species, e.g. *C. exostemma* and *C. pannosa.* This has resulted in the multiple naming of these species, with each variant being awarded species status, further compounding nomenclatural problems.

The pantropical genus *Caesalpinia*, as traditionally circumscribed, includes approximately 120 to 130 species and contains 25 generic names as synonyms (Table 1). Faced with this number of species and the complicated nomenclature associated with many of them, an initial survey of all species and related literature was carried out in a search for suites of charcters that might indicate natural biological groups. Once these were more or less established, one group, corresponding principally to the genus *Poincianella* Britton & Rose, was selected for detailed analysis as it seemed to contain the most diverse elements of *Caesalpinia sens. lat.* and was apparently endemic to the neotropics. Britton and Rose (1930), however, only worked on North American taxa and it was clear that Bentham and Hooker's (1865) *Caesalpinia* section *Caesalpinaria*, from both Central and South America, also belonged to the *Poincianella* group.

Having recognised the broad morphological groups it was now possible to carry out a preliminary cladistic analysis of these in an attempt to show evolutionary relationships

Table 1. **Generic names associated with *Caesalpinia* since 1753**

GENUS	AUTHOR(S)	DATE	CURRENT PLACEMENT (LEWIS, 1994)
BALSAMOCARPON	Clos	1846	BALSAMOCARPON
BIANCAEA	Todaro	1860	Unplaced Old World taxon
BONDUC	Mill.	1754	CAESALPINIA subgenus Guilandina
BRASILETTIA	(DC.) Kuntze	1891	CAESALPINIA: Brasilettia Group
CAESALPINIA	L.	1753	CAESALPINIA
CAMPECIA	Adans.	1763	Unplaced Old World Taxon = Biancaea
CINCLIDOCARPUS	Zoll.	1846	Unplaced Old World Taxon
CLADOTRICHIUM	Vogel	1837	Pomaria Group aff. Hoffmannseggia
COULTERIA	Kunth	1824	CAESALPINIA: Russellodendron Group
ERYTHROSTEMON	Klotzsch	1844	CAESALPINIA: Erythrostemon Group
GUAYMASIA	Britton & Rose	1930	CAESALPINIA: Brasilettia Group
GUILANDINA	L.	1753	CAESALPINIA subgenus Guilandina
HOFFMANNSEGGIA	Cav.	1798	HOFFMANNSEGGIA
LARREA	Ortega	1797	HOFFMANNSEGGIA + Pomaria Group
LARREA	Cav.	1800	ZYGOPHYLLACEAE
LIBIDIBIA	(DC.) Schlecht.	1830	CAESALPINIA: Libidibia Group
MELANOSTICTA	DC.	1825	Pomaria Group aff. Hoffmannseggia
MEZONEURON	Desf.	1818	CAESALPINIA subgenus Mezoneuron
MOPARIA	Britton & Rose	1930	HOFFMANNSEGGIA
MOULLAVA	Adans.	1763	MOULLAVA
NICARGO	Britton & Rose	1930	CAESALPINIA: Russellodendron Group
POINCIANA	L.	1753	CAESALPINIA s.s. + DELONIX
POINCIANELLA	Britton & Rose	1930	CAESALPINIA: Poincianella Group
POMARIA	Cav.	1799	Pomaria Group aff. Hoffmannseggia
REICHARDIA	Roth	1821	PTEROLOBIUM
RUSSELLODENDRON	Britton & Rose	1930	CAESALPINIA: Russellodendron Group
SCHRAMMIA	Britton & Rose	1930	CAESALPINIA: Poincianella Group
TARA	Molina	1789	CAESALPINIA: Russellodendron Group
TICANTO	Adans.	1763	Unplaced Old World taxon
WAGATEA	Dalzell	1851	MOULLAVA

between them (see section on phylogeny). It is "*Poincianella* A", "*Poincianella* B" and *Erythrostemon* in "Clade E" of the cladistic analysis that have been revised in the present work. No formal reinstatement of genera is proposed in this thesis and these three elements of Clade E should presently be considered as informal groups with intermediate taxa holding them together, e.g. *C. eriostachys*, in *Poincianella* A, from Central America and Mexico, seems closely related to *C. pluviosa sens. lat.*, in *Poincianella* B, from Brazil. Similarly, *C. fimbriata* and *C. calycina* in South America link *Poincianella* B with *Erythrostemon*, the latter expanded here to include several species erroneously placed by Burkart (1936) in *Caesalpinia* section *Pomaria*, which in the strict sense is much more closely related to the genus *Hoffmannseggia* (see phylogeny section). The core of this study has thus grown to become a revision of the *Poincianella–Erythrostemon* "group" of *Caesalpinia sens. lat.* and all the species in this group are strictly neotropical.

Having selected the *Poincianella–Erythrostemon* "group" for revision, a more detailed morphological analysis was carried out of all the species within it. In total 56 taxa in 47 species are dealt with in this revision, and the geographical distribution of these taxa ranges from the southern United States of America to southern Chile, from the Andes in Bolivia and Peru to the caatinga vegetation of eastern Brazil, and across Mexico and Central America (from El Salvador to Costa Rica). The revision is based on the study of approximately 10,000 herbarium specimens and on field work carried out in Mexico, Central America (El Salvador, Honduras and Guatemala), Cuba and Brazil from 1987 to 1992. Many new characters have been observed from living material but, to date, only 31 of the 56 taxa considered in this account have been studied in the field. In 1992 two months were spent in eastern Brazil studying the sexual systems of two bee pollinated species in *Poincianella* B with the aim of trying to better understand the relationship between the floral morphologies of the species and their pollinators (see Appendix 2).

TAXONOMIC HISTORY

Caesalpinia has an extremely complex taxonomic history (Table 2) and the associated nomenclature highlights the difficulties that previous workers have had with the generic limits. This confusion will persist, in part, until all species have been studied in detail and the group revised across its geographical range. The present work clears up the nomenclatural confusion of several neotropical *Caesalpinia* species. It also lays the ground work (see phylogeny section) for the possible reinstatement of four to nine names at generic rank in the future. It would be premature and, in my view, unwise to do this here.

The genus *Caesalpinia* was formally named by Linnaeus in 1753 in honour of Andrea Caesalpino (1524/5–1603), Italian botanist, philosopher and physician to Pope Clement VIII. Linnaeus described four species: *Caesalpinia brasiliensis*, *C. crista*, *C. sappan* and *C. vesicaria*. *C. brasiliensis* is the type species of the genus and has been recently lectotypified on a Plumier plate by Lewis and Reveal in Jarvis et al. (1993). The other three species described by Linnaeus remain in *Caesalpinia sens. lat.* but are distantly related to *C. brasiliensis* and do not belong in *Caesalpinia sens. strict.* In 1753, Linnaeus also published the name *Poinciana pulcherrima*, now *Caesalpinia pulcherrima*, the well-known tropical garden ornamental thought to have originated in central Guatemala or NW Mexico. This butterfly-pollinated species is presumed to be a member of *Caesalpinia sens. strict.* based on the presence of stem armature, the calyx morphology and the seed and fruit type, and is thus excluded from the revision presented here. A third genus, *Guilandina*, was also described by Linnaeus in 1753 and contained three species: *G. bonduc* (the common pantropical scrambling shrub with prickly fruits and globose seeds), *G. moringa* and *G. dioica*, but these latter two are now excluded from *Caesalpinia sens. lat.* P. Miller (1754) proposed the genus *Bonduc* but this is equivalent to *Guilandina* L.

Adanson (1763) described three more related genera, namely *Campecia*, *Moullava* (the correct name for *Wagatea* Dalzell) and *Ticanto*. *Moullava* is monotypic and *M. spicata* is, for now, considered by me as distinct from *Caesalpinia sens. lat.*

Molina (1789) introduced the genus *Tara* with one species, *T. tinctoria* (a synonym of *Caesalpinia spinosa*) excluded from my *Poincianella–Erythrostemon* group and phytochemically grouped with *Brasilettia* and allies (Kite and Lewis, in press).

Table 2. **The main classifications of *Caesalpinia* and related taxa**

LINNAEUS (1753)	DE CANDOLLE (1825)	BENTHAM & HOOKER (1865)	BRITTON & ROSE (1930)	LEWIS (1994)
CAESALPINIA	**CAESALPINIA**	**CAESALPINA**		**CAESALPINIA**
	sect. Nugaria (OW) (Ticanto)	sect. Nugaria (OW)	**TICANTO** (OW)	
	sect. Sappania (OW) (Campecia)	sect. Sappania (OW) (Biancaea)	**BIANCAEA** (OW)	
	sect. Libidibia	sect. Libidibia	**LIBIDIBIA**	*LIBIDIBIA* group
			GUAYMASIA	*BRASILETTIA* group (Guaymasia)
	sect. Brasilettia		**BRASILETTIA**	
		sect. Caesalpinaria	**POINCIANELLA**	*POINCIANELLA* group*
			SCHRAMMIA	(Schrammia)
		sect. Erythrostemon	**ERYTHROSTEMON**	*ERYTHROSTEMON* group
			CAESALPINIA s.s.	*CAESALPINIA s.s.* group (Poinciana p.p.)
		sect. Cinclidocarpus (OW)		
			NICARGO	*RUSSELLODENDRON* group
	COULTERIA	sect. Coulteria	**RUSSELLODENDRON**	(Nicargo)
			TARA	(Tara)
		sect. Balsamocarpon (SA)		(Coulteria)
	POMARIA	sect. Pomaria (Cladotrichium)		
GUILANDINA	**GUILANDINA**	sect. Guilandina	**GUILANDINA**	subgenus *GUILANDINA* (Bonduc)
POINCIANA	**POINCIANA**	**[POINCIANA = DELONIX]** (OW)	**POINCIANA**	
	MEZONEURON (OW)	**MEZONEURON** (OW)		subgenus *MEZONEURON*
	HOFFMANNSEGGIA	**HOFFMANNSEGGIA** (Melanosticta)	**LARREA** Ortega, non Cav. (Hoffmannseggia) (Pomaria)	**HOFFMANNSEGGIA** s.s. (Moparia)
	MELANOSTICTA (OW)		**MOPARIA**	*POMARIA* GROUP (Cladotrichium) (Larrea Ortega, p.p.) (Melanosticta) (OW)
	REICHARDIA (OW)	**PTEROLOBIUM** (Reichardia)		**PTEROLOBIUM** (OW) (Reichardia)
		PELTOPHORUM (Brasilettia p.p.)		**BALSAMOCARPON** (SA)
				MOULLAVA (OW) (Wagatea)
OW = Old World, SA = South America, * = including Caesalpinia sect. Caesalpinaria pp. (excluding *C. pulcherrima*)				UNPLACED OLD WORLD TAXA: Biancaea (Campecia); Ticanto; Cinclidocarpus.
Genera in boldface, synonyms in brackets				

herb:table2 gwl(dmc)

The genus *Larrea* Ortega (1797), based on *L. glauca*, has been rejected versus *Larrea* Cav. (1800), the latter in the Zygophyllaceae. In 1798, Cavanilles described *Hoffmannseggia* (for discussion on the correct spelling of this generic name see Brummitt and Ross, 1974) and this is the genus into which several species of *Larrea* Ortega are now placed. B.B. Simpson and I consider *Hoffmannseggia* to be a distinct genus of mainly self-compatible herbs and shrublets although some taxa intermediate with the *Poincianella* group do exist (e.g. *H. intricata* and *H. virgata*). Nevertheless, *Hoffmannseggia*, as currently understood by me, excludes several species described in it from Central America and Mexico and all species dealt with by Brummitt and Ross (1974) in Africa.

In 1799 Cavanilles described a second genus, *Pomaria* which most subsequent workers have placed in synonymy under *Hoffmannseggia*, thus generating much confusion for modern-day Flora writers. Although not dealt with in the revision presented in this work, I consider *Pomaria* to be distinct from *Hoffmannseggia* based on the presence of surface glands on the leaflets and the lack of a tuft of hairs at the base of the standard petal in the former.

In 1818, Desfontaines described *Mezoneuron* based on *M. glabrum*. Currently recognised as a subgenus of *Caesalpinia* (Herendeen and Zarucchi, 1990) this Old World taxon of some 35 species has no extant member in the New World. Fossil evidence (Herendeen and Dilcher, 1991) indicates, however, that species of *Mezoneuron* once grew in North America (see phylogeny section). I consider *Mezoneuron* to be closely related to *Caesalpinia sens. strict.* based on floral morphology.

Coulteria Kunth (1824), with no designated type, was the next published generic name that has become associated with *Caesalpinia sens. lat.* Like several names before it, it is excluded from the *Poincianella–Erythrostemon* group revised here.

De Candolle (1825) was the first to present an overview of what had gone before and give some structure to *Caesalpinia* in which he recognised four sections: *Nugaria*, *Brasilettia*, *Sappania* and *Libidibia*, based mainly on different fruit types with some correlated seed characters. All but section *Sappania* he suggested might be more appropriately recognised at the rank of genus. His section *Nugaria* contained three species and included Adanson's genus *Ticanto*. Section *Brasilettia* contained two species, section *Libidibia* one (*Caesalpinia coriaria* (Jacq.) Willd.) and section *Sappania* (in which he included Adanson's *Campecia*) a rag-bag of ten species from various parts of the tropics,

only two of which are dealt with in this revision, namely *C. glandulosa* Bert. and *C. exostemma* DC. Six species were considered insufficiently known for sectional placement at the time and these included *C. echinata* Lam. and *C. pluviosa* DC., both considered in the present work. De Candolle accepted the generic status of *Guilandina*, *Coulteria*, *Poinciana*, *Mezoneuron*, *Reichardia* (described by Roth in 1821 but subsequently rejected versus *Pterolobium* R. Brown ex R. Wight & Arnott), *Hoffmannseggia* and *Pomaria* and described a new genus, *Melanosticta*, to accommodate the African *M. burchellii*, which I consider to be closely related to New World *Pomaria* species. In 1830, Schlechtendal raised De Candolle's section *Libidibia* to generic rank without adding any additional species.

Vogel (1837) proposed the genus *Cladotrichium* in which he recognised four species, all based on Sellow collections from Brazil. The genus was said to be closely related to *Melanosticta* and *Hoffmannseggia* and in my view it certainly links the African *Melanosticta* with Mexican and Central American *Pomaria* by a suite of floral and foliage characters, not least of which the black glands, ± valvate calyces and herbaceous habit.

In 1844 Klotzsch removed *Caesalpinia gilliesii* (Hook.) D. Dietr. into his monotypic genus *Erythrostemon*. This moth-pollinated species is very distinctive by its cream-yellow flowers with long-exserted red stamens and is considered in this revision as a specialised member of the expanded *Erythrostemon* group.

Three more new genera were to be added to the list of *Caesalpinia* relatives before Bentham and Hooker's reappraisal in 1865. *Cinclidocarpus* Zollinger was described in 1846, *Balsamocarpon* Clos. in the same year and *Biancaea* Todaro in 1860.

Bentham and Hooker in their Genera Plantarum (1865) took a broad view and recognised *Caesalpinia* with ten sections and placed it in their tribe *Eucaesalpinieae*. Of the ten sections, *Nugaria*, *Sappania* and *Libidibia* had already been presented as sections in the system of De Candolle. In addition, the genera *Guilandina*, *Erythrostemon*, *Pomaria*, *Balsamocarpon*, *Coulteria* and *Cinclidocarpus* were all down-ranked to sections. *Caesalpinaria* was added as a new section. The genus *Biancaea* Todaro was included in section *Sappania*; *Cladotrichium* Vog. was included under section *Pomaria*. *Mezoneuron* was retained as a good genus restricted to the Old World. The circumscription of *Hoffmannseggia* was expanded to include *Melanosticta* in synonymy thus making it an amphiatlantic taxon. *Poinciana* was also retained as a genus but now excluded elements of

Caesalpinia sens. lat. Overall this was a pragmatic approach to a difficult group of plants and Bentham and Hooker's system was largely followed until the work of Britton and Rose (1930). Significantly, Bentham and Hooker removed *Caesalpinia* section *Brasilettia* DC. from *Caesalpinia* and placed it in synonomy under *Peltophorum* Vog, but this was an error.

Baker (1878), in Hooker's Flora of British India, presented three subgenera in *Caesalpinia*: *Guilandina*, *Eucaesalpinia* and *Cinclidocarpus*.

In 1891, Kuntze raised De Candolle's section *Brasilettia* to generic rank with *B. brasiliensis* (L.) O. Kuntze as the type species. The basionym, *Caesalpinia brasiliensis* L. is, however, the lectotype of *Caesalpinia* so that *Brasilettia* must be referred back to *Caesalpinia* by lectotypification. Taubert in Engler and Prantl's Pflanzenfamilien (1892) adopted the system of Bentham and Hooker unchanged.

The first noteworthy Flora for the neotropics that contained several *Caesalpinia sens. lat.* species was Bentham's account of the Leguminosae in Martius' Flora Brasiliensis (1870). Of the 17 species dealt with by Bentham, ten are referable to the present revision of the *Poincianella–Erythrostemon* group. Of these ten species, *C. peltophoroides* Benth. (= *C. pluviosa* DC. var. *peltophoroides* (Benth.) G.P. Lewis of my account), *C. calycina* Benth. and *C. gardneriana* Benth. were described as new.

Typical of the taxonomic confusion witnessed in neotropical *Caesalpinia* is that perpetrated by E.M. Fisher. In 1892 he published a revision of the genus *Hoffmannseggia* in North America, accepting *Pomaria* Cav. and *Melanosticta* DC. as generic synonyms (thus following Torrey and Gray, 1840). One year later, in a paper in the Botanical Gazette, he united *Hoffmannseggia* with *Caesalpinia* and provided new combinations in *Caesalpinia* for all the taxa "even if extreme species in the two genera seem to be so unlike each other". Pivotal to his argument for doing this was *Hoffmannseggia caudata* Gray, which he argued has more of the characters of *Caesalpinia palmeri* S. Wats. (in my *Poincianella* group) than any species of *Hoffmannseggia*. Placement of the species in *Caesalpinia* was, however, no good reason for Fisher to argue that all other *Hoffmannseggia* species be moved to *Caesalpinia* and this action only served to confuse subsequent workers. Recently (Ulibarri, 1979; Simpson and Lewis, unpublished) *Hoffmannseggia* has again been accepted as a distinct genus although several species originally described in it should now be placed elsewhere, principally in *Pomaria sens.*

strict. It is the few intermediate species, linking otherwise natural biological groups, together with the resulting character overlap between the groups, that has resulted in much taxonomic lumping into *Caesalpinia* which in many modern Floras is consequently very heterogeneous.

Rose (1911) described two new species of *Poinciana* and made six new combinations based on *Caesalpinia* basionyms. Seven of this total of eight species are treated in the *Poincianella* group of this thesis.

In 1920 Standley adopted Bentham's broad circumscription of *Caesalpinia* and listed 24 species in his Trees and Shrubs of Mexico. *C. phyllanthoides* was described as new. Where necessary, new combinations were made based on Rose's *Poinciana* names. Fourteen names (representing twelve species) of those listed by Standley are dealt with by me as belonging to the *Poincianella* group.

Britton and Wilson (1924) in their account of the botany of Porto Rico [= Puerto Rico] and the Virgin Islands listed four species in *Caesalpinia*, of which only *C. glandulosa* Bert. is dealt with here.

One of the important legume works for Mexico and Central America to be published in the 20th century is that of Britton and Rose (1930). Their understanding of biological groups was based on good field observations and collections but they have been strongly criticised for their 'splitter' approach to species taxonomy and for the proliferation of monotypic "one organ" genera. Their revision of *Caesalpinia sens. lat.*, and especially their segregate genus *Poincianella*, provided the basis for the revision presented here. They proposed several new genera, segregated from *Caesalpinia sens. lat.*: *Moparia*, *Schrammia* (which overcame Fisher's earlier dilemma by providing a monotypic genus for *Caesalpinia caudata* (Gray) Fisher), *Nicargo*, *Russellodendron*, *Guaymasia* and *Poincianella*. They also accepted at generic rank *Larrea* Ortega (a rejected name versus *Larrea* Cav. in the Zygophyllaceae) with *Hoffmannseggia* and *Pomaria* placed in synonymy; *Libidibia*; *Ticanto*; *Tara*; *Brasilettia*; *Poinciana*; *Caesalpinia sens. strict.*; *Erythrostemon*; *Biancaea* and *Guilandina*. They recognised 34 species of *Poincianella*; in my revision 21 of these are retained as good species, one (*P. ortegae*) is rejected from the group and considered as a *Pomaria*, one (*Poincianella tampicoana*) is reduced to a subspecies of *Caesalpinia exostemma* and 11 names are reduced to synonymy within the group, most notably six Cuban taxa. One species of *Erythrostemon*, *E. gilliesii*, a species

naturalised after cultivation in Texas, New Mexico and Arizona was considered by Britton and Rose.

Britton and Killip (1936) followed the segregates of Britton and Rose (1930) but there are surprisingly few *Caesalpinia sens. lat.* species in Colombia and no *Poincianella* or *Erythrostemon* species.

In the same year, Burkart (1936) revised *Caesalpinia* for Argentina. This excellent piece of work contributed significantly to our understanding of *Caesalpinia* in South America and added two new species: *C. argentina* Burk. and *C. cromantha* Burk. (= *C. fimbriata* in my revision). Burkart followed Bentham and Hooker (1865) and Taubert (1894) and recognised a broad circumscription for *Caesalpinia* with most of the segregates of Britton and Rose (1930) in synonymy. Burkart's revision included fourteen species, mostly assigned to sections within *Caesalpinia*. Nine of these are dealt with in my revision: *C. gilliesii*, *C. trichocarpa*, *C. mimosifolia*, *C. coulterioides*, *C. cromantha* (= *C. fimbriata*), *C. coluteifolia*, *C. exilifolia*, *C. argentina* and *C. floribunda* (= *C. pluviosa* var. *pluviosa*). The majority of these (all but *C. gilliesii* and *C. floribunda*) were erroneously referred to section *Pomaria* (Cav.) Benth. & Hook. because of the dark punctate glands present especially on the foliage. They are, however, not equatable with *Pomaria sens. strict.* (see cladistic analysis) which in Burkart's revision should include only C. *epunctata* and *C. rubicunda*. In my revision all the species referred by Burkart to section *Pomaria* are placed in the *Erythrostemon* group. Of the remaining Argentinian species recorded by Burkart, *C. pumilio* is excluded from my revision because of its persistent calyx lobes on the mature lunate fruits and the distinctly dimorphic stamens (Fig. 69) characters that suggest a closer affinity with the genus *Hoffmannseggia*. *C. stuckertii* (Fig. 70) was unplaced to section by Burkart but in his observations he suggested that it might constitute a new section with the Mexican species *C. sessilifolia* as a close relative, a view with which I entirely agree. Both *C. stuckertii* and *C. sessilifolia* are excluded from my revision.

Since Burkart's revision (1936) all subsequent treatments of *Caesalpinia* in the neotropics have also returned to Bentham and Hooker's broad circumscription of the genus. McBride (1943) in his Flora of Peru went even further and (unfortunately) included *Hoffmannseggia* as a synonym of *Caesalpinia*. Only the introduced *C. gilliesii*

(of the 14 species dealt with by McBride) is covered by my revision and it is apparent that Peru, like Colombia has a paucity of species in the *Poincianella–Erythrostemon* group.

Standley and Steyermark (1946) dealt with 14 species of *Caesalpinia sens. lat.* for Guatemala and in a note under the genus comment that "Britton and Rose divided North American species into about ten genera, some of which might have a good basis for generic segregation, but it seems more satisfactory to treat the group in the sense it was maintained by Bentham. What practical or sentimental advantage results from its division into smaller units, often of only a single species each, is not apparent". This somewhat contradictory statement was an easy way out for Flora writers presented with the difficult task of dealing with *Caesalpinia*, but clouded over any relationships between species , especially as the treatment of Standley and Steyermark presented the species alphabetically and not systematically. No new species were proposed in their work.

León and Alain in their account of the legumes of Cuba (1951) recorded 26 species of *Caesalpinia* for the island. Twelve of these fall within the *Poincianella* group of this work. *Caesalpinia hermeliae* León is unique amongst these twelve species in never having been given a combination in the genus *Poincianella*. Ten of the twelve species were considered by León and Alain to be endemic to Cuba; with only *C. eriostachys* and *C. glandulosa* having a wider geographical range. The ten endemic species are here reduced to three: *C. guanensis*, known only from the type specimen collected from the western tip of Cuba is conspecific with *C. gaumeri* from the Yucatan Peninsula of Mexico (Map 13) and is thus not endemic; *C. nipensis* is distinct and restricted to the eastern end of the island (Map 14); *C. myabensis* (here including *C. subglauca*, *C. hornei*, *C. clementis* and *C. hermeliae*) has bipinnate leaves; and *C. pinnata* (including *C. oblongifolia* and *C. savannarum*) differing from *C. myabensis* only by its once pinnate leaves.

Wiggins (1980) presented four native species of *Caesalpinia* for Baja California, all belonging to the *Poincianella–Erythrostemon* group. *C. placida* is seemingly most closely related to Argentinian species of the group while I consider the other three to be conspecific so that *C. arenosa* and *C. californica* are here given as synonyms of *C. pannosa*.

Of the 21 species recorded for the Flora de la Española [i.e. Haiti and the Dominican Republic] by Liogier (1985) only two, *C. pellucida* and *C. glandulosa* occur in the *Poincianella–Erythrostemon* group.

1987 saw three further contributions to neotropical *Caesalpinia*. Ulibarri (1987) sank *C. fisheriana* and *C. rosulata* into synonymy under *C. trichocarpa*. McVaugh (1987) in his Flora Novo Galiciana dealt with five species placed by me in the *Poincianella-Erythrostemon* group: *C. caladenia*, *C. eriostachys*, *C. exostemma*, *C. mexicana* and *C. laxa* (under which he included some specimens referable to *C. hintonii* and *C. macvaughii*). Lewis (1987) recorded twelve species of *Caesalpinia sens. lat.* for the Brazilian state of Bahia, nine of which belong to the *Poincianella-Erythrostemon* group. Two of these, *C. paraensis* and *C. peltophoroides* I now consider as varieties of *C. pluviosa*.

Ulibarri (1991) in his notes on *Caesalpinia* in Paraguay, recognised the morphological variation seen in some species and chose to place six names in synonymy under two species: *C. pluviosa* and *C. fimbriata*. I had already, independently arrived at the conclusion that *C. cromantha* and *C. bangii* should be treated as synonyms of *C. fimbriata*. With respect to *C. pluviosa*, I am of the opinion that Ulibarri's synonymy, although a pragmatic approach to a difficult problem, has lumped too many names. There is some information to be gained about speciation patterns from recognising apparently distinct variants with different geographical distributions as varieties of *C. pluviosa* and I recognise six in my account. In 1991 Ulibarri, in a separate paper, described a new species, *C. ancashiana*, from Peru and it is included, by me, in the *Poincianella-Erythrostemon* group.

Contreras (1991) published an account of *Caesalpinia* in the Mexican state of Guerrero. Nine of the 20 species dealt with by him belong to the *Poincianella-Erythrostemon* group. *C. epifanioi*, endemic to Guerrero, had been described by Contreras in 1987. *C. macvaughii* from Guerrero and Michoacan, discussed in Contreras' thesis was validly published by Contreras and Lewis in 1992. One species, thought by Contreras to be closely related to *C. mexicana*, has still to be given a name, but due to a lack of material is not dealt with here. Contreras sank *C. acapulcensis* into *C. caladenia*; I keep the two separate. With that one exception, he and I more or less agree on the delimitation of all other species in western Mexico and we described a second new species, *C. coccinea* in 1994.

Recently, Barreto Valdés (1992) published a paper on the Cuban species *C. myabensis* and reduced four closely related species to varieties of it (*C. clementis*, *C. hermeliae*, *C. hornei* and *C. subglauca*). I had gone a stage further and placed all these as

synonyms of *C. myabensis* before seeing Barreto's paper. Our taxonomy is essentially the same but the foliage characters she used to recognise the five varieties seem both weak and overlapping, especially given the huge variation known to occur in the foliage of several other *Caesalpinia* species. I do not uphold her infraspecific taxa in this treatment.

There is much work still to do before all species of *Caesalpinia sens. lat.* can be accurately assigned to infrageneric taxa or segregate genera. It seems likely that a combination of the sections of Bentham and Hooker together with some of De Candolle's genera and some of Britton and Rose's genera will ultimately represent the most natural hierarchy. For the present work the most pragmatic approach is considered to be the recognition of informal groups consisting of related taxa. It is possible, even probable, that the *Poincianella–Erythrostemon* group revised here will need to be further segregated at sectional, subgeneric or even generic rank in the future.

MORPHOLOGY

In the section on morphology that follows, emphasis will be given to the *Poincianella-Erythrostemon* group, but characters will also be discussed in context of their variation within *Caesalpinia sens. lat.* Infrageneric groups of *Caesalpinia sensu lato* delimited in the section on phylogeny, are frequently referred to in the following text.

Habit. Species of the *Poincianella-Erythrostemon* group vary from woody-based perennial herbs and shrublets of low stature (e.g. *C. angulata* (Fig. 62D), *C. caudata, C. nelsonii* and *C. phyllanthoides*) to multiple-stemmed shrubs or treelets, to large single-trunked trees up to 30 metres tall with a trunk diameter of 50 centimetres (e.g. *C. eriostachys*). Most species are small trees of 3 to 10 metres tall. *Caesalpinia caudata* has a thick woody root-stock with several stems arising from ground level; *C. phyllanthoides* is a rhizomatous, colony-forming, woody-based herb to 80 cm tall. *C. angulata* is usually a sprawling shrub, while *C. pannosa* can be prostrate or sometimes more or less scandent. *C. glandulosa* is often scandent (the climbing habit assisted by recurved prickles), but no species of the *Poincianella-Erythrostemon* group become robust woody climbers as found in *Caesalpinia* subgenus *Guilandina* and subgenus *Mezoneuron*. *Caesalpinia nipensis* can reproduce vegetatively from young shoots which arise spontaneously from subsurface stolons.

Tree crowns vary in shape, sometimes within a species — *C. yucatanensis* may produce an inverted cone-shaped crown, a round compact crown or an open crown with crooked branching. The inverted cone-shaped crown is also seen in *C. caladenia* and *C. eriostachys*. The mature trunks of older specimens of *C. pluviosa* and *C. eriostachys* are frequently intricately fluted, a feature also encountered in the genera *Cenostigma* and *Haematoxylon* of the *Caesalpinia* group of tribe Caesalpinieae.

Bark, Wood and Stems. Bark type and colour of the *Poincianella-Erythrostemon* group varies between groups of species, and sometimes within a single species depending on the maturity of the individual. Bark colour varies from greyish-white (e.g. *C. hintonii* (Fig. 32B)) to black (e.g. mature specimens of *C. echinata*). Various shades of grey, green and brown are common and orange bark is sometimes seen (e.g. specimens of *C. echinata*). The bark is occasionally mottled various shades of grey (e.g. some specimens of *C.*

FIG. 1. Bark types: **A** *C. hughesii* (*MacQueen et al.* 409); **B** *C. hughesii*, main trunk (*MacQueen et al.* 409); **C** *C. caladenia* (*Lewis et al.* 2072); **D** *C. pannosa* (*Lewis et al.* 2033); **E** *C. pluviosa* var. *cabraliana* (*Lewis et al.* 2019); **F** *C. pluviosa* var. *paraensis* (*Lewis et al.* 1629); **G** *C. ferrea* (*Libidibia* group), cultivated tree, Rio de Janeiro Bot. Gard. (unvouchered).

eriostachys). Pustular lenticels are common on the younger stems of many species and usually contrast in colour with the bark — white lenticels on dark brown or greyish-green bark are common (Fig. 1A). They may be randomly scattered or arranged in vertical rows. Bark consistency usually alters with the age of the plant (most noticeable on species that mature to large trees). Most species that are shrubs or small trees have a smooth, somewhat shiny bark. This frequently splits vertically and the paper-thin outer bark then peels back to reveal a green under-bark (e.g. *C. pannosa*, Fig. 1D). The greyish-white bark of *C. hintonii* is sometimes corky and the outer-bark occasionally exfoliates. Large specimens of *C. eriostachys* have vertically fissured bark which is scaley and rough while younger specimens usually have smooth bark. The bark of mature trees of *C. echinata* often breaks off in large irregular plates. No species in the *Poincianella-Erythrostemon* group produce the 'leopard-skin' bark of the ironwood species in "*Libidibia* B" (Fig. 1G). Generally the outer bark slash is green, the inner slash creamish or off-white. Cut trunks and branches frequently smell of garden peas or beans. The heartwood of mature tree species is brown or black (e.g. *C. exostemma* and *C. gaumeri*).

Branches may be knobbly and warted (as in *C. coccinea*) but are more often smooth (except where pustular lenticels are present). Young stems are smooth and terete except in *C. angulata* which takes its name from the angled stems. Stem colour varies with age, but in some species young branchlets are pink or reddish. A few species have a tendency for zig-zag stems (e.g. *C. palmeri*), but this character is not consistent. In very arid habitats some taxa (e.g. *C. palmeri*) produce woody brachyblasts (short shoots) from which the leaves and inflorescences arise. Two species in the *Poincianella-Erythrostemon* group form prickles or thorns: *C. glandulosa* is armed with recurved woody prickles which are scattered along the stems (Fig. 44C), with pairs of larger prickles arising from the nodes; *C. echinata* produces short, woody, upturned thorns that develop from woody protuberances on branches and young tree trunks (Fig. 54C); more mature specimens lack thorns suggesting a defensive function on younger plants. Elsewhere in *Caesalpinia sens. lat.*, thorns and prickles are widespread and their presence characterizes *Caesalpinia sens. strict.* (including *C. pulcherrima*, *C. pauciflora* (Fig. 71) and *C. cassioides* (Fig. 72), subgenus *Mezoneuron* and subgenus *Guilandina*. Young stems may be glabrous or pubescent, glandular or eglandular and variation in indumentum is often seen within a species.

Tree architecture, bark type, stem and trunk exudates all require detailed study throughout *Caesalpinia sens. lat.*

Stipules. Stipules of most species of *Caesalpinia sens. lat.* are early caducous and, in consequence, have been little studied. Stein (1982) demonstrated that stipular development in *Caesalpinia* displays two patterns. Although his survey was based on only 12 species it is noteworthy that his findings support the recognition of the *Poincianella-Erythrostemon* group. Only two species, *C. mexicana* and *C. gilliesii*, show a proleptic stipule development, i.e. the stipule covers the leaf with which it is associated until emergence from the bud. The other 10 species surveyed lack proleptic stipules and display the 'typical' relationship in which the stipules are initiated as lateral domains of the leaf primordium, smaller than the main portion of the leaf, and maintain a subordinate position during the entire ontogeny of the organ. This, apparently more common stipule development, was found in *Guilandina, Brasilettia, Libidibia* A, *Russellodendron* and *Caesalpinia sens. strict.*, but not in the *Poincianella-Erythrostemon* group. A wider survey is necessary to determine if this difference is consistent. Within the *Poincianella-Erythrostemon* group stipules have been observed for about half the species and are commonly ovate-orbicular or triangular-ovate in shape and rarely exceed 10 mm in length. Their margins are frequently ciliate-fimbriate and sometimes glandular. Those of *C. calycina* and *C. coulterioides* are broadly orbicular, somewhat foliaceous and cordate-auriculate at the base. The 10 to 12 mm long stipules of *C. gaumeri* are petaliferous and spathulate-cucullate. Those of *C. pyramidalis* are linear-spathulate to broadly spathulate, those of *C. angulata* are lanceolate-triangular and of *C. eriostachys* and *C. pellucida* filiform (the latter type apparently unusual in the group). Stipules are best studied on seedlings and young flush foliage of mature plants.

Leaves. Leaves of *Caesalpinia sens. lat.* are alternate and in most species bipinnate. In the *Poincianella-Erythrostemon* group, *Caesalpinia pinnata* (Fig. 39A) and *C. marginata* (Fig. 45A) have pinnate leaves, an apparent reduction from the bipinnate state. There is a strong tendency in the groups for bipinnate leaves to be imparipinnate (i.e. they end in a single terminal pinna), but there are exceptions and sometimes imparipinnate and paripinnate (ending in a pair) states both occur in one species (e.g. in *C. eriostachys*).

Elsewhere in *Caesalpinia sens. lat.*, bipinnate, paripinnate leaves are common in *Guilandina, Brasilettia* and *Caesalpinia sens. strict.*

Pinnae may be opposite or alternate. In *C. ancashiana* the leaves are reduced to three pinnae — an opposite pair plus a single terminal pinna. Leaves of *C. gilliesii* can have as many as 15 pairs of pinnae plus a single terminal pinna. All other species of the *Poincianella-Erythrostemon* group have pinnae numbers that fall between those of *C. ancashiana* and *C. gilliesii*.

Leaflets are alternate or opposite and species normally have one or the other, but sometimes both configurations occur within a species and even on a single leaf. On the pinnate leaf of *C. marginata* leaflets may be opposite or alternate; in *C. myabensis* leaflets of the lateral pinnae are opposite but of the terminal pinna alternate. In *C. pluviosa* the situation is reversed with the lateral pinnae having alternate leaflets and the terminal pinna opposite ones. Nevertheless, within the *Poincianella-Erythrostemon* group species can be broadly divided into those that have opposite leaflets and those that have alternate ones. With the exception of *C. eriostachys, C. gaumeri* and *C. pellucida*, all Central American, Mexican and Caribbean species have mostly opposite leaflets. So do all the species from western South America (Peru, Bolivia, Argentina, Chile and Paraguay). All Brazilian species have alternate leaflets, except for *C. calycina* and *C. marginata* (mentioned above). Leaflet number ranges from 3 to 31 per pinna for species with alternate leaflets and from 4 to 22 (i.e. 2 to 11 pairs) for those with opposite leaflets. The exception is *C. caudata* (Fig. 68) which has a terminal pinna which subtends 8 to 20 pairs of opposite leaflets and is considerably longer than the lateral pinnae which have 3 to 7 pairs. Leaflets are sessile or subsessile with short petiolules.

Leaflet blades may be fleshy with all but the primary vein obscure (e.g. in *C. pannosa, C. phyllanthoides, C. palmeri, C. calycina, C. fimbriata, C. coulterioides* and *C. angulata*). Where the secondary venation is distinct it is always brochidodromous. *C. marginata* has a prominent marginal or submarginal vein (Fig. 45A & B). *C. caudata* is unique in the *Poincianella-Erythrostemon* group in having a more or less palmate primary venation pattern (i.e. several main veins from the leaflet base) (Fig. 68B) but the secondaries are brochidodromous. Some species have strongly coriaceous leaflets (e.g. *C. marginata, C. pinnata* and *C. laxiflora*). Leaflet size and shape vary greatly both between and within species, and leaflets on young plants or on new terminal shoots of older plants

are often considerably larger than those on more mature plants and branches. Sometimes leaflet size varies greatly on a single terminal branchlet of one plant (e.g. *C. pluviosa* var. *sanfranciscana*, see frontispiece). Leaflet vestiture can also vary greatly within a population of one species (e.g. *C. exostemma* and *C. pannosa*) and the presence of pubesent or glabrous leaflets has not been found to be a useful species marker even though it has been widely used to segregate taxa by several workers in the past.

In the species descriptions of this revision the term leaflet gland has been applied in a rather general way and includes both external glands and internal secretory cavities. Recently Lersten and Curtis (in press) surveyed the leaf anatomy of 65 species of *Caesalpinia sensu lato* and *Hoffmannseggia* with emphasis given to secretory structures. It is a pity that their findings were not available to me when I carried out my cladistic analysis of the *Caesalpinia* group as their results are taxonomically significant. They recognise three types of secretory structure: external glands; internal cavities and idioblastic cells in 46 species of the 65 analysed; in 43 species these structures were distributed mutually exclusively. They found that external glands were most widely distributed throughout *Caesalpinia sensu lato* and *Hoffmannseggia* species and suggested that the simplest explanation for such a distribution is to assume that they can evolve easily from either trichomes or ordinary epidermal parenchyma cells, and that they have therefore evolved independently among various taxa. *C. gilliesii* was unique in their survey in having partially embedded nodular structures (which are apparently glandular) along the abaxial margin of the leaflets. These structures are thus morphologically intermediate between gland and cavitiy. They are clearly visible on herbarium material as dark punctate 'glands'.

Lersten and Curtis found that true internal cavities are restricted to species of *Poincianella* (*C. bracteosa, C. eriostachys, C. gaumeri, C. microphylla, C. pyramidalis, C. pluviosa* var. *peltophoroides* and *C. pluviosa* var. *pluviosa* of their survey). They suggested that, although these structures do not define *Poincianella*, any additional species that may be found with cavities can be strongly suspected of belonging to it. The internal secretory cavity seems to be a significant taxonomic character.

Idioblastic cells were found in 31 of the species examined by Lersten and Curtis and these, too, seem to be useful taxonomic characters. They were completely lacking in

all species of *Poincianella* surveyed and only present in *C. trichocarpa* of *Erythrostemon*. They are widespread in *Caesalpinia sens. strict., Guilandina, Brasilettia* and *Mezoneuron*.

In the *Poncianella-Erythrostemon* group I have noted five basic gland patterns: 1) glands totally lacking on any part of all leaflets; 2) glands always lacking from leaflet blades but present along the margin (although these occasionally obscure); 3) glands usually lacking on leaflet blades but nearly always present along the margin of at least some leaflets of each leaf; 4) subepidermal glands (equivalent to the secretory cavities of Lersten and Curtis) scattered over the leaflet blade and usually most evident on the lower surface of young leaflets as black or dark red dots, sometimes also present along the margin; 5) external stalked glands often scattered over leaflet blades, with subepidermal glands sometimes also present.

The five patterns are somewhat geographically correlated throughout the *Poincianella-Erythrostemon* group:

Pattern 1 is found in species 1 to 8 of this revision (all from Mexico or Central America) and also in *C. exilifolia, C. coluteifolia* and *C. angulata* from western South America. Some species which normally have eglandular leaflets very occasionally have some leaflets with glandular margins and thus generally fit pattern 1 with rare specimens conforming to pattern 2. Included amongst these are *C. exostemma, C. yucatanensis, C. laxa, C. hintonii, C. epifanioi* and *C. melanadenia*, all from Mexico and Central America, and *C. glandulosa* from Cuba and Hispaniola.

Pattern 2 is found in *C. coccinea* and *C. macvaughii* from Mexico, and *C. marginata* from western South America.

Pattern 3 is restricted to South American *Erythrostemon* species and to the closely related *C. placida* from Baja California. The marginal glands may be placed in crenulate depressions, e.g. in *C. fimbriata* and *C. mimosifolia* or be submarginal as in *C. argentina. C. trichocarpa* sometimes has glands on the blade lower surface as well as on the margin. Other species having pattern 3 include *C. calycina, C. gilliesii*, C. *ancashiana* and *C. coulterioides*.

Pattern 4 is found widely in Mexican, Central American, Caribbean and Brazilian *Poincianella* species and most are medium to large trees. Included are *C. eriostachys, C. gaumeri, C. pinnata, C. myabensis, C. pellucida, C. nipensis, C. pyramidalis, C.*

bracteosa, C. pluviosa and *C. echinata. C. caudata* from south eastern USA has some leaflets of each plant with subepidermal glands.

Pattern 5 is exclusive to Brazilian species. *C. gardneriana, C. laxiflora, C. microphylla* and *C. pyramidalis* often have short-stalked glands on the lower surface of juvenille leaflets. These occasionally persist on mature leaflets.

Single, gland-tipped, cone-shaped appendages are frequently found below each leaflet pulvinule and these may also be found clustered into a corona at the pinnae insertions on the leaf rhachis. These structures are common in many Mexican and Central American taxa but less so in South American species (they occur in *C. calycina*). There is some correlation between their presence and a lack of leaflet glands but the two are not mutually exclusive.

Inflorescence. Inflorescences are commonly erect, axillary or terminal pedunculate racemes with 10 to about 140 pedicellate flowers. Less often they are reduced, few-flowered congested racemes and in extreme cases may be single-flowered (e.g. some specimens of *C. palmeri*). In a few species inflorescences arise from leafy brachyblasts (short woody shoots) e.g. in some specimens of *C. palmeri, C. melanadenia, C. placida* and *C. caladenia*. Racemes are frequently aggregated into terminal panicles. In some taxa racemes and panicles occur on the same tree (e.g. *C. exostemma, C. coccinea* and *C. hughesii*), in others young plants have long racemes while older plants have congested panicles (in *C. yucatanensis*, for example, woody panicles are more common on old senescent trees). Inflorescences are occasionally leaf-opposed as in *C. mimosifolia, C. trichocarpa* and *C. gardneriana*. In *C. glandulosa* they are ramiflorous. The long slender racemes of *C. hintonii* may be erect or pendulous on different plants and are usually aggregated into showy terminal panicles.

Field observations suggest that many species in the *Poincianella-Erythrostemon* group open two or three flowers per raceme each day and that the flowers remain open for 12 to 24 hours (see Appendix 2 for further comment). Herbarium specimens tend to support this as a generality within the group. Andromonoecy is known in *C. calycina* (see Appendix 2) and may be more common than previously thought within the group. Dioecy has not been found to date in the *Poincianella-Erythrostemon* group but is known to occur in *Caesalpinia* subgenus *Guilandina* and in the *Brasilettia* group.

Flowers. Most species in the *Poincianella-Erythrostemon* group are bee-pollinated (personal observation and inference based on flower type), but *C. gilliesii* (Figs. 3A and 57) is known to be moth-pollinated and *C. exostemma* is apparently pollinated by humming birds and carpenter bees (Fig. 24D & E). The bee flowers vary greatly between groups of species and range from the large yellow flowers of *C. calycina* (Fig. 2C) to the much smaller pinkish-red flowers of *C. hintonii* (Fig. 2D) and *C. melanadenia*. Different bee genera tend to be associated with the different flower types: large solitary carpenter bees being important pollinators of the large yellow-flowered species and smaller *Centris* species often pollinating the small, pink-flowered taxa. Within *Caesalpinia sens. lat.* the range of flower morphologies (Figs. 2, 3 and 4) and associated pollinator types is even more diverse. *C. pulcherrima* is butterfly-pollinated, and it is suspected that *C. bahamensis* might be bat-pollinated. Conversely, in some genera of the tribe Caesalpinieae there has been remarkable convergence in flower morphology resulting from an evolution of floral characters cannalised by similar pollinator type (e.g. note the similarity between the flowers of *C. nelsonii* [Fig. 62E] and *Haematoxylum brasiletto* [Fig. 62C]).

All species in the *Poincianella-Erythrostemon* group have pedicellate flowers with pedicels varying in length from a few millimetres to 3 cm. Nearly all have a zone or articulation somewhere along their length (ranging from directly below the calyx to 12 mm below), but a few species lack this (e.g. *C. calycina, C. gilliesii, C. caudata* and apparently *C. coluteifolia*). In species that have the articulated pedicel the zone of articulation is usually above the middle but occasionally it is in the lower quarter as in *C. macvaughii*. It is also well below the middle in *C. pyramidalis* var. *pyramidalis*, a taxon with an overall facies very similar to *C. pluviosa* var. *sanfranciscana* which has pedicels articulated just below the calyx. Unfertilized flowers often abscise at this point of articulation leaving a semi-persistent pedicel peg on the inflorescence rhachis.

Calyces have five imbricate sepals with the lowest one usually being larger and cucullate. These abscise from the calyx tube or hypanthium prior to fruit maturation (in distinct contrast to *Hoffmannseggia* species in which the complete calyx persists to fruit maturation [Fig. 4B]). All flowers have five petals which are imbricate with the 'standard' petal innermost as is typical in subfamily Caesalpinioideae. The uppermost lateral petals,

FIG. 2. Flower diversity in *Caesalpinia sens. lat.*: **A** *C. exostemma* subsp. *exostemma* (*Poincianella*) (*Lewis & Hughes* 1709); **B** *C. pluviosa* var. *sanfranciscana* (*Poincianella*) (unvouchered); **C** *C. calycina* (*Erythrostemon*) (unvouchered); **D** *C. hintonii* (*Poincianella*) (*MacQueen et al.* 428); **E** *C. pulcherrima* (*Caesalpinia s.s.*) (unvouchered); **F** *C. bahamensis* (*Caesalpinia s.s.*) (*Lewis* 1853).

FIG. 3. Flower diversity in *Caesalpinia sens. lat.*: **A** *C. gilliesii* (*Erythrostemon*) (unvouchered); **B** *C. sclerocarpa* (*Libidibia*) (*Lewis et al.* 1800); **C** *C. velutina* (*Brasilettia*) (*Lewis & Hughes* 1713); **D** *C. spinosa* (*Russellodendron*) (unvouchered).

FIG.4. **A** *Hoffmannseggia glauca*, flower, Texas; **B** *H. humilis*, fruits, Puebla, Mexico; **C** *H. oxycarpa*, flower, Texas; **D** *C. (Pomaria) jamesii*, flower, Texas. Photos.: B.B. Simpson.

equal in shape and size, are usually larger than the lower pair. Petal colour varies from creamish-yellow to deep pinkish-scarlet or salmon pink. Most species have bright yellow petals with the standard petal often flecked, streaked or network-veined orangish-red. The standard petal is very variable in size, shape and vestiture between species. This variation is taxonomically significant, both within the *Poincianella-Erythrostemon* group and between other groups of *Caesalpinia sens. lat.* (Fig. 5) and would seem to be closely associated with pollinator type. Considering the species treated in the present revision, important characters have been found on the inner surface of the standard petal claw, particularly the presence or absence of an apical thickening or appendage which when present may act as a tactile pollinator guide or, more probably, as a mechanical block to potential nectar robbers. The standard claw appendage is most pronounced in *C. exostemma* subsp. *exostemma* (Fig. 13A) as a glabrous thickened ridge at the claw apex, and in *C. yucatanensis* subsp. *yucatanenis* (Fig. 4 [Phylogeny]) where it is a large, folded, pubescent flange. A few species lack a claw to the standard (e.g. *C. gilliesii* (Fig. 57F), *C. glandulosa* (Fig. 44E) and *C. angulata* (Fig. 67E)) and *C. caudata* has a highly reduced claw (Fig. 68E). In *C. mexicana, C. phyllanthoides, C. pannosa* and *Poincianella robinsoniana* the standard claw lacks a ridge or appendage but is usually pubescent. In species 20 to 24 (*C. eriostachys, C. gaumeri* (Fig. 5Q), *C. pinnata* (Fig. 5R), *C. myabensis* and *C. pellucida*) the claw is thickened and somewhat inrolled and usually pubescent but there is no apical appendage. Similarly, in species 37 to 45, mostly from western South America, but including *C. placida* (Fig. 5V) from Baja California, the small claws lack an appendage but are usually pubescent (having at least a small tuft of hairs on their inner surface) and sometimes inrolled (e.g. *C. mimosifolia* [Fig. 59J]). *C. echinata* (Fig. 5L), from Brazil, has an unelaborated claw with a small tuft of hairs on the inner surface; *C. calycina* has no appendage and lacks pubescence. Most taxa in the Mexican and Central American species 5 to 19 have some sort of apical appendage or ridge on the standard claw, but *C. exostemma* subsp. *tampicoana* lacks any elaboration, and it is often obscure in *C. palmeri*. In species where it is present it may be pubescent or glabrous. In *C. melanadenia* the pubescent ridge is sometimes composed of overlapping, fin-shaped or crested appendages (Fig. 35H). In the essentially Brazilian species (species 28 to 33 in the revision), the claw is generally thickened and longitudinally grooved with a glandular or eglandular ridge at the apex, but there is no ridge or appendage in *C.*

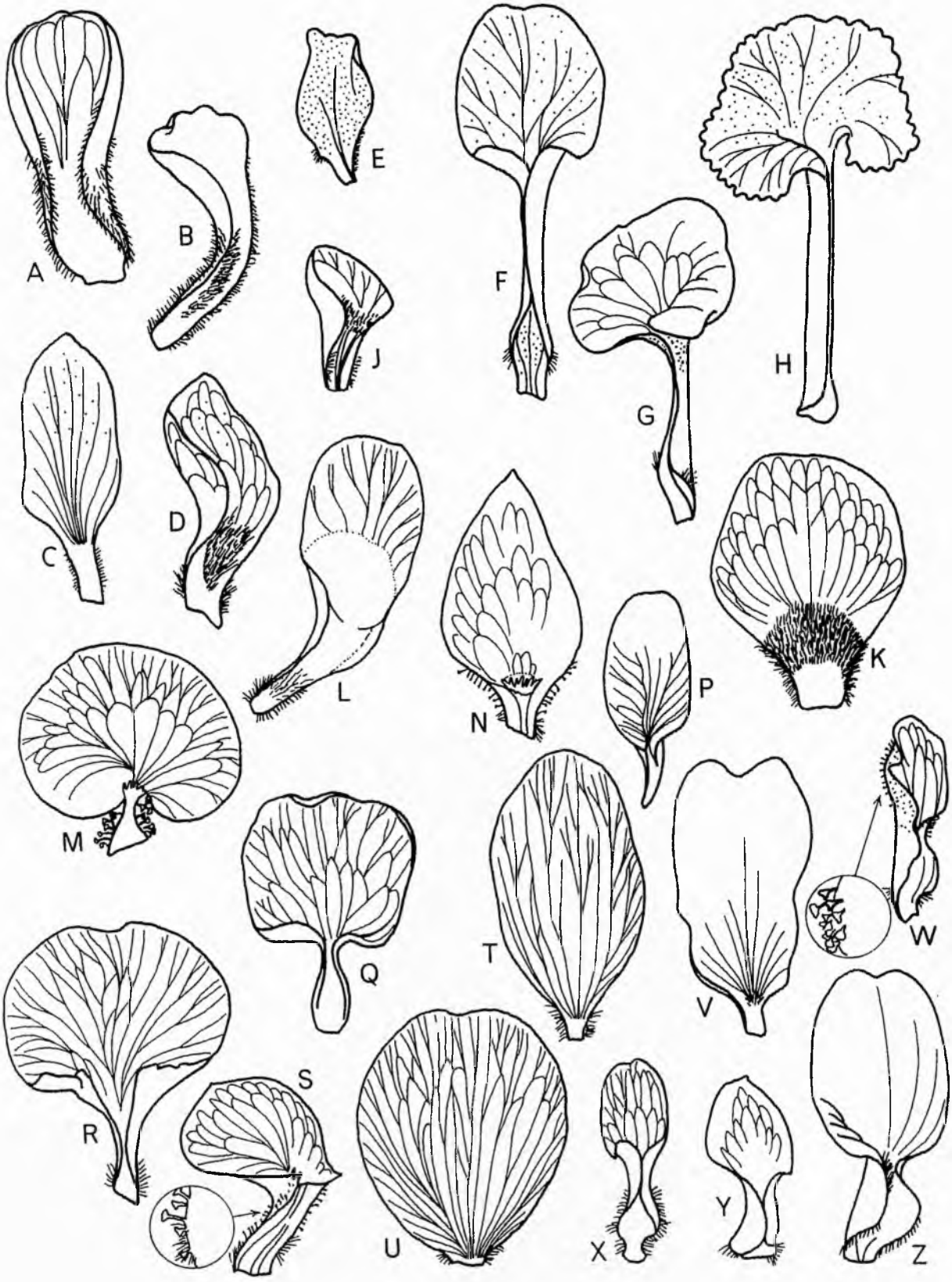


FIG. 5. Standard petals in *Caesalpinia sensu lato*. **A** *C. velutina* (Brasilettia group) x 9; **B** *C. pumila* (Brasilettia group) x 9; **C** *C. sphaerosperma* (subgenus Guilandina) x 9; **D** *C. bonduc* (subgenus Guilandina) x 9; **E** *C. barahonensis* (Caeselpinia s.s.) x 9; **F** *C. rosei* (Caesalpinia s.s.) x 6; **G** *C. pauciflora* (Caesalpinia s.s.) x 9; **H** *C. pulcherrima* (Caesalpinia s.s.) x 6; **J** *C. hildebrandtii* (subgenus Mezoneuron) x 9; **K** *C. sclerocarpa* (Libidibia group) x 9; **L** *C. echinata* (Poincianella group) x 6; **M** *C. nelsonii* (Poincianella group) x 9; **N** *C. epifanioi* (Poincianella group) x 6; **P** *C. pannosa* (Poincianella group) x 6; **Q** *C. gaumeri* (Poincianella group) x 6; **R** *C. pinnata* (Poincianella group) x 6; **S** *C. laxiflora* (Poincianella group) x 6; **T** *C. trichocarpa* (Erythrostemon group) x 6; **U** *C. exilifolia* (Erythrostemon group) x 6; **V** *C. placida* (Erythrostemon group) x 6; **W** *C. epunctata* (Pomaria group) x 6; **X** *C. melanosticta* (Pomaria group) x 9; **Y** *C. fruticosa* (Pomaria group) x 9; **Z** *C. ortegae* (Pomaria group) x 9. Drawn by author.

microphylla. The apical ridge in *C. bracteosa* is elaborated into a dentate glandular appendage on either side of the central groove.

Floral secretory structures in *Caesalpinia sens. lat.* appear to be as taxonomically significant as leaflet secretory structures. A preliminary survey found three main types: glandular hairs, secretory idioblasts and nodular secretory ducts. These findings are presented in a co-authored paper to be published in Advances in Legume Systematics, part 6 - Structural Botany (in press; see Appendix 1). Secretory ducts are found in a group of related species from Brazil, namely *C. microphylla, C. pluviosa* var. *peltophoroides, C. pluviosa* var. *sanfranciscana* and *C. pyramidalis* var. *pyramidalis* and also in *C. eriostachys* from Central America and Mexico. This suggests an affinity between these North and South American taxa that is also seen in macromorphology. Glandular hairs are widespread throughout *Caesalpinia sens. lat.* and several related genera, but are lacking in the two species of *Caesalpinia sens. strict.* surveyed. All but *C. nipensis* in the *Poincianella* group have glandular hairs on at least some part of their flowers. It seems possible that *C. nipensis*,from Cuba, is misplaced in the *Poincianella* group and its relationship with species of *Caesalpinia sens. strict.* needs to be examined further, as both have subepidermal idioblasts in their flowers, a relatively uncommon feature in the *Caesalpinia* group. *C. nipensis* has paripinnate leaves and a fruit type that also suggest a relationship with *Caesalpinia sens. strict.*

The androecium is composed of ten stamens made up of an inner whorl of five stamens which are opposite the petals and an outer whorl of five opposite the sepals. The filaments are usually densely hairy near their bases and the hairs of each are interwoven so as to form a staminal pseudosheath which effectively closes access to the calyx tube. The vexillary stamen is usually narrowed and glabrous at its base thus forming a small window on either side between itself and the adjacent stamens which allows access to the calyx tube. These fenestrae coincide with the position of insertion of the standard petal claw which must be raised by a flower visitor before access to the nectar can be achieved.

The gynoecium is unicarpellate, sessile or shortly stipitate and inserted into the base of the calyx tube. The ovary is either glabrous or has a wide range of indumentum types. In the *Poincianella* group, individuals of the same species can have glandular or eglandular ovaries. The style is filiform and usually curved upwards towards its apex.

The *Poincianella-Erythrostemon* group has three basic stigma types:

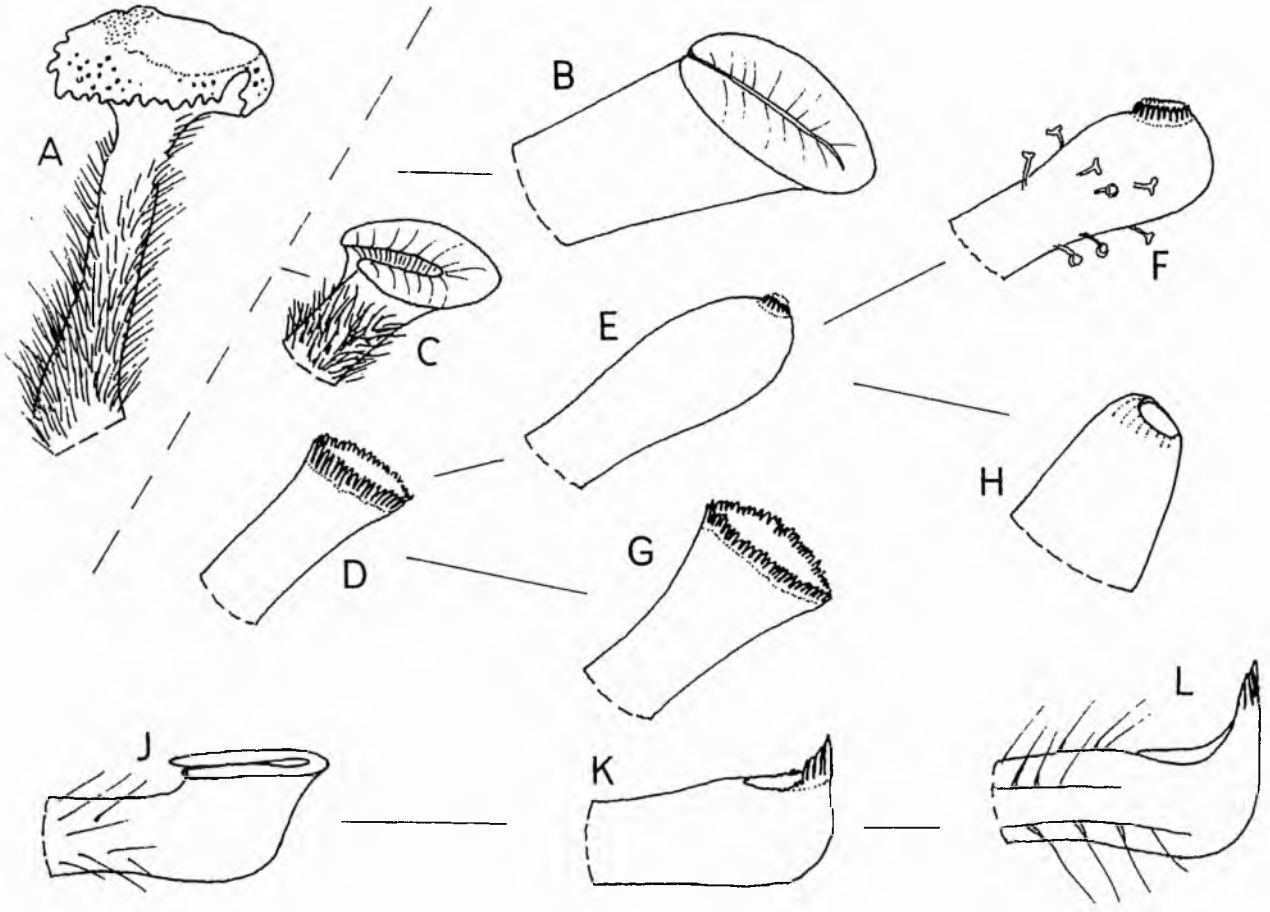


FIG. 6. Stigma types in *Caesalpinia sensu lato* and *Peltophorum*. **A** *Peltophorum dubium* x 18; **B** *C. (Guilandina) sphaerosperma* x 40; **C** *C. (Brasilettia) velutina* x 20; **D** *C. buchii* x 40; **E** *C. (Libidibia) sclerocarpa* x 24; **F** *C. (Poincianella) eriostachys* x 18; **G** *C. pulcherrima* x 40; **H** *C. (Poincianella) pannosa* x 40; **J** *Hoffmannseggia (Pomaria) burchellii* x 40; **K** *C. (Pomaria) epunctata* x 40; **L** *C. (Pomaria) ortegae* x 40. Drawn by author.

1) A terminal unfringed pore, e.g. in *C. pannosa* (Fig. 6H), *C. exostemma* (Fig. 13B), *C. hughesii, C. coccinea, C. laxa, C. hintonii* and *C. melanadenia.*

2) A terminal, tubular or funnel-shaped, fringed chamber with the fringe cells acting as a circular pollen-comb; this the most common form in the group and in *Caesalpinia sens. strict.* (Fig. 6D & G).

3) A terminal or, more often, subterminal, bulbous chamber narrowing to a fringed pore, e.g. in *C. eriostachys* (Fig. 6F), *C. gaumeri* and all of the Brazilian species except for *C. calycina.*

All stigmas of tribe Caesalpinieae studied by Owens (1990) were found to be of the wet, non-papillate (WN) form, following the classification of Heslop-Harrison (1981). The WN stigma form is also known in tribe Cassieae of Caesalpinioideae (Owens and Lewis, 1989) in which differences in gross stigma morphology, and especially size, shape and surface ornamentation of the sterile hairs, which fringe the porate opening to the stigmatic surface, were found to aid separation of the genera *Cassia, Chamaecrista* and *Senna.* All the stigmas examined by Owens (1990) in the Caesalpinieae are crateriform, i.e. they have a stigmatic cup which is either flask-shaped and opens as a narrow pore, funnel-shaped tapering from a wide opening, or shallow with the stigmatic chamber exposed. The exact relationship between these stigma types and pollinators is still to be explored. (See Appendix 2 for detailed comment on *Caesalpinia calycina*). Elsewhere in the *Caesalpinia* group of tribe Caesalpinieae other stigma morphologies occur in taxa not included in the survey of Owens (1990). *Hoffmannseggia* and *Pomaria* (Fig. 6J-L), for example, have laterally placed stigmas with a partial fringe of cells around the stigma opening. *Brasilettia* species have stigmas with a V-shaped aperture on their adaxial margin with a marked adaxial suture on the ovary which runs into the stigmatic groove (Fig. 6C) (Contreras, 1991). A complete survey of stigma types in the *Caesalpinia* group is highly desirable and should prove to be taxonomically instructive.

Fruit. The fruits of the *Poincianella-Erythrostemon* group are straight, curved, falcate or lunate, elastically dehiscent legumes (Fig. 7L & M, Fig. 8A & B) which scatter their seeds as the valves split apart and then usually twist or roll up (e.g. Fig. 21E). The valves vary in texture from chartaceous to coriaceous or subligneous (the latter common in north east Brazilian species). The valve vestiture varies from glabrous to densely pubescent and from

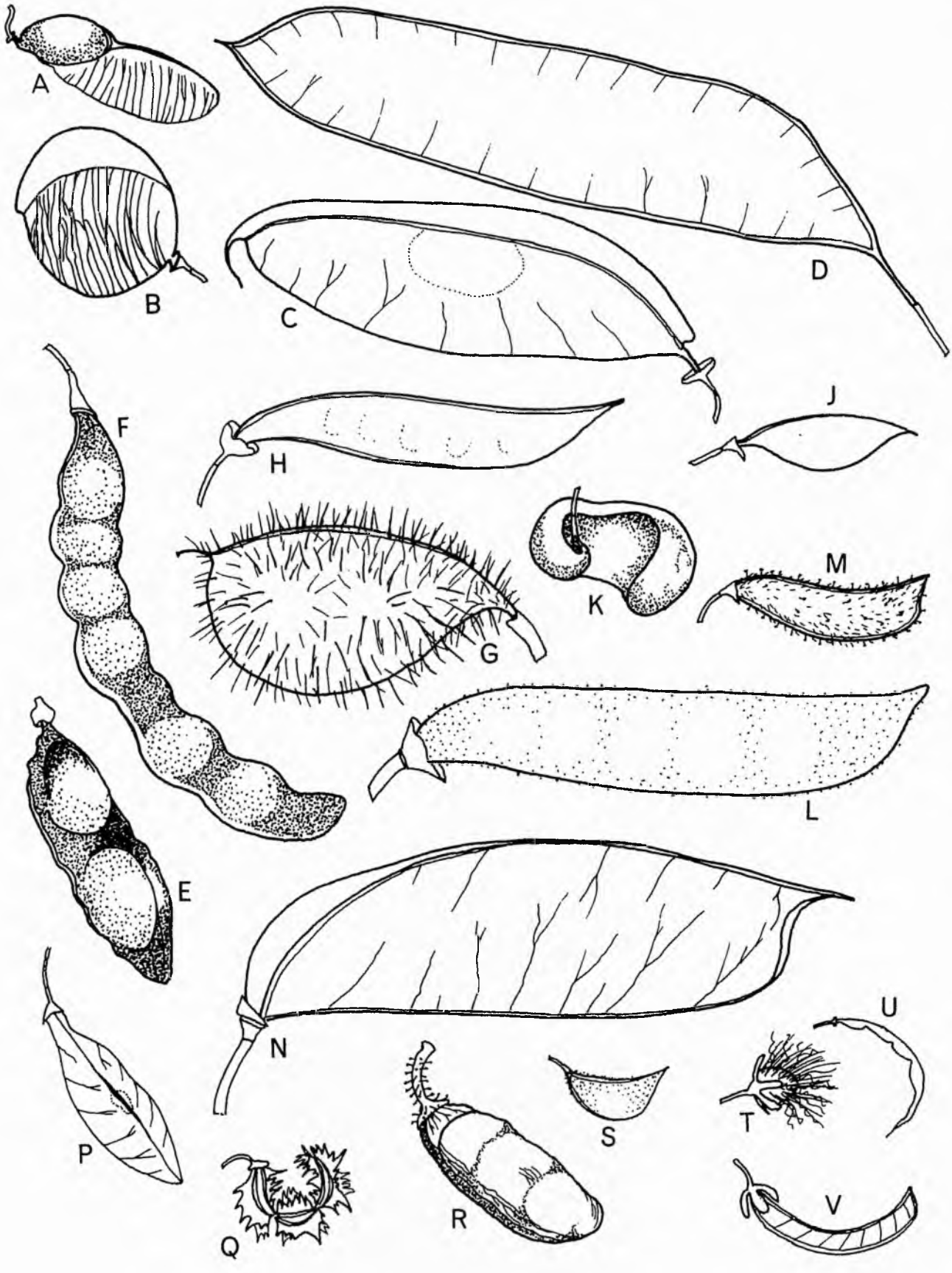


FIG. 7. Fruit diversity in the *Caesalpinia* group of tribe Caesalpinieae. **A** *Pterolobium stellatum*; **B** *C. (Mezoneuron) scortechinii*; **C** *C. (Mezoneuron) cucullata*; **D** *C. (Brasilettia) violacea*; **E** *Moullava spicata*; **F** *C. (Russellodendron) cacalaco*; **G** *C. (Guilandina) bonduc*; **H** *C. bahamensis;* **J** *.C. erianthera;* **K** *C. (Libidibia) coriaria*; **L** *C. (Poincianella) exostemma*; **M** *C. (Poincianella) palmeri*; **N** *Cenostigma macrophyllum*; **P** *Haematoxylum brasiletto*; **Q** *Lophocarpinia aculeatifolia*; **R** *Balsamocarpon brevifolium*; **S** *C. (Pomaria) jamesii*; **T** *Zuccagnia punctata*; **U** *Stenodrepanum bergii*; **V** *Hoffmannseggia glauca*. All x 1. Drawn by the author.

FIG. 8. Fruits in *Caesalpinia sens. lat.*: **A** *Caesalpinia calycina (Erythrostemon)*, Bahia, Brazil (unvouchered); **B** *C. nicaraguensis (Poincianella)*, Nicaragua (*Hawkins* 4, photo.: C.E. Hughes); **C** *C. bahamensis (Caesalpinia s.s.)*, Cuba (*Lewis* 1853); **D** *C. pulcherrima (Caesalpinia s.s.)*, Guatemala (*Lewis & Hughes* 1715); **E** *C. bonduc (Guilandina)*, Madagascar (unvouchered); **F** *coriaria (Libidibia)*, El Salvador (*Lewis et al.* 1745).

eglandular to densely glandular. Pods of different individuals in a population of one species of some *Poincianella* species may be glabrous and eglandular or pubescent and densely glandular (Fig. 17E & F). The fruits of *C. echinata* have spiny protuberances which persist to maturity (Figs. 54M and 55D.

In *Caesalpinia sens. lat.* and related genera fruits are very variable in morphology and were used by DeCandolle, Bentham & Hooker, and Britton & Rose to recognise sections and segregate genera (Figs. 7 and 8). Most species of *Guilandina* have spiny fruits which dehisce along the upper margin of the suture (Figs. 7G and 8E). In the *Russellodendron* group the fruits (Figs. 7F and 12B) are indehiscent as they are in the *Libidibia* group (Figs. 7K and 8F) where they are also thick and woody with a pulpy, tannin rich, mesocarp and septate, coriaceous endocarp. *Mezoneuron* has indehiscent, chartaceous or subcoriaceous, fruits with the upper margin of the suture winged (Fig. 7B & C). This subgenus of *Caesalpinia* is restricted to the Old World although fossil fruits from south eastern USA and from England show that the taxon was more widespread in the Palaeocene - early Eocence (Herendeen & Dilcher, 1991). Personal observation in Madagascar shows that the *Mezoneuron* fruit type can be successfully distributed by both wind and water. *Brasilettia* has laterally compressed, *Albizia*-like fruits which are indehiscent and lack any marginal wing (Figs. 7D and 12A).

Seeds. In the *Poincianella-Erythrostemon* group seeds (Fig. 9) are laterally compressed, have a hard testa which lacks a pleurogram but often has fracture lines, and in all known cases lack endosperm (although this is sometimes present in related groups, e.g. *Russellodendron*). The funicle is short, the hilum punctiform, flush or recessed, the embryo straight, and the cotyledons well developed. The testa is usually glossy and varies in colour from creamish-yellow through bright yellow, orangish-yellow and buff-ochre to dark chocolate brown. Occasionally seeds have blotches or streaks of a colour that contrasts with the base colour, e.g. *C. hughesii* has yellow-ochre seeds with red bands or streaks. In *Caesalpinia sens. lat.* seeds appear to be more or less consistent to group, e.g. those of *Brasilettia* are distinct (Fig. 9G & H), as are those of *Guilandina* which are unusual in being spheroidal (Fig. 8E).

FIG. 9. Seeds: **A** *Caesalpinia aff. mexicana* x1 (*MacQueen et al.* 427); **B** *C. exostemma* subsp.*exostemma* (*Lewis & Hughes* 1753); **C** *C. yucatanensis* subsp. *chiapensis* (*Hughes* 1353); **D** *C. eriostachys* (*Hughes* - 30/83/01); **E** *C. microphylla* (*Coradin et al.* 5941); **F** *C. calycina* (*Carvalho* 2693); **G** *C. (Brasilettia) sp.* (Rico & Windsor-Shaw s.n.); **H** *C. (Brasilettia) velutina* (*Lewis & Hughes* 1713). Scale bar = 0.5 cm

Seedlings. Most seedlings of *Caesalpinia sens. lat.* observed to date are phaneroepigeal with foliar cotyledons (Figs. 10 and 11), as is common in other Caesalpinioideae (Duke & Polhill, 1981), and this is the pattern in the *Poincianella-Erythrostemon* group. The subgenus *Guilandina* is odd in having epigeal germination and in being cryptocotylar. Eophyll type and position vary between groups of species of *Caesalpinia sens. lat.*and appear to be taxonomically instructive. Species in *Poincianella* A generally have the first eophyll pinnate and the second alternate and bipinnate (Figs. 10A-C and 11C), but this can vary, e.g. in *C. mexicana* the second eophyll is sometimes pinnate. *C. eriostachys* is unusual amongst Central American *Poincianella* species in having the first and second eophylls bipinnate with the leaflets of each pinna alternate (Fig. 11A). *Caesalpinia pulcherrima* (in *Caesalpinia sens. strict.*) has the two eophylls opposite and pinnate (Fig. 11B).

The foliaceous cotyledons are usually rounded at the apex, cordate at the base and are tardily caducous. Smith and Scott (1985) found that a greater diversity of cotyledon venation patterns were found in tribe Caesalpinieae than in any other tribe of Caesalpinioideae, and this diversity in the tribe as a whole is also reflected in the variation found within species of *Caesalpinia sens. lat.* This adds support for segregation at the intrageneric level.

Nyctinastic leaf movements ('sleep' movements associated with light changes) are known to occur widely in Leguminosae but few systematic accounts have looked at these as a taxonomic character at the species level . Lavin (1988) found them useful in his account of *Coursetia*, and Luckow (1993) studied them in species of *Desmanthus* . In all *Poincianella* species studied to date the leaf rhachides and leaflets droop in the evening (Fig. 10C), and the upper surfaces of each leaflet pair are folded together. The response in *C. pulcherrima* (of *Caesalpinia sens. strict.*) is similar to that seen in the *Poincianella* group but *C. velutina* of the *Brasilettia* group is different in that the drooped leaflets have the lower surface of each pair folded together. Simpson (unpublished data) has noted three nyctinastic responses in a range of *Caesalpinia s.l.* and *Hoffmannseggia* species. Her findings show that *C. platyloba* (in the *Brasilettia* group) conforms to the pattern noted in *C. velutina*. *C. coluteifolia* and *C. exilifolia* in the *Erythrostemon* group fold their leaflets upwards with their upper surfaces folded together; *C. gilliesii* in the same group also folds its leaflets upwards but

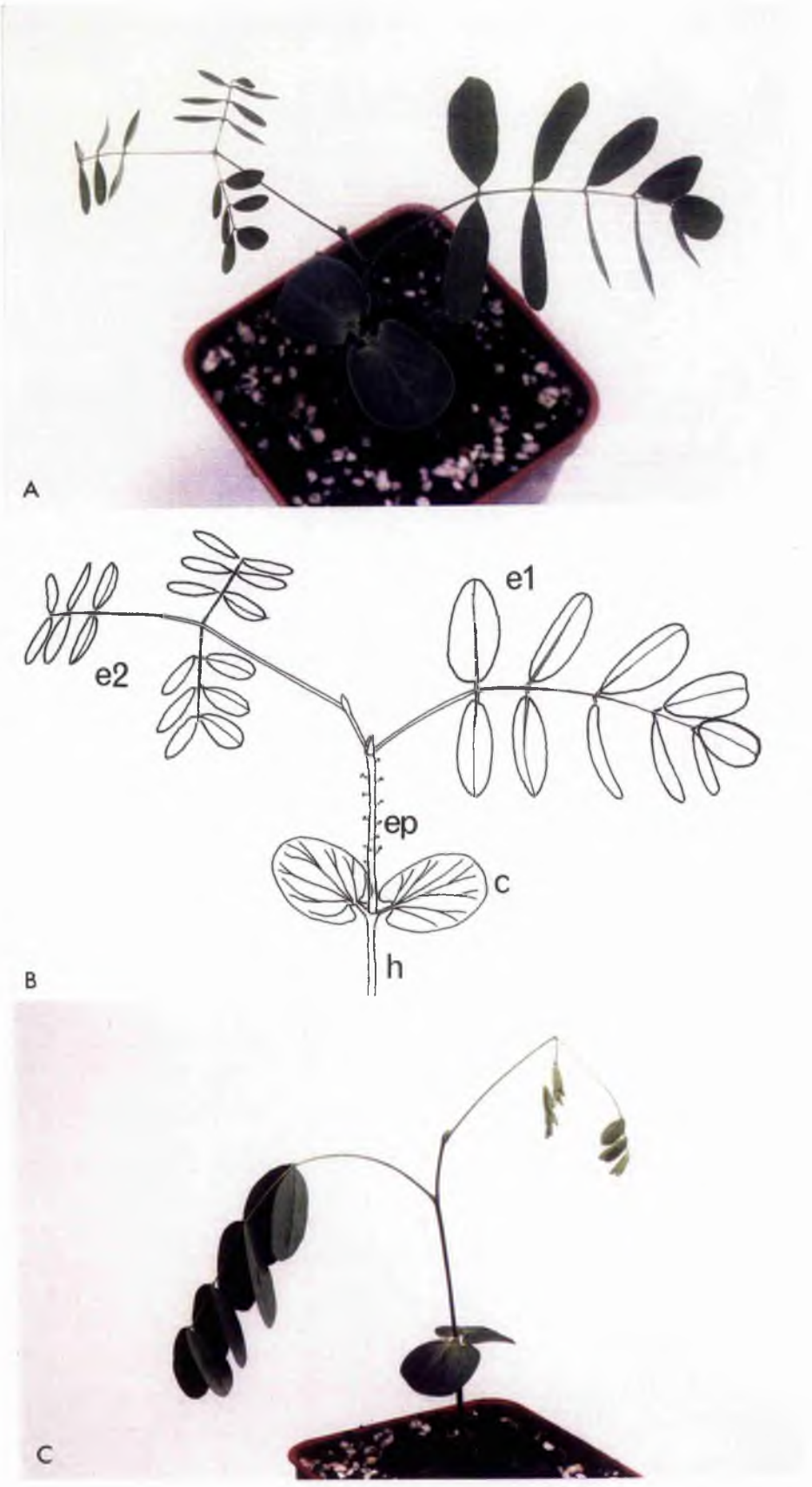


FIG. 10. Seedlings: **A** *C. hughesii* (*Lewis et al.* 1795); **B** diagramatic representation of **A**, c = cotyledon, e = eophyll, ep = epicotyl, h = hypocotyl; **C** *C. coccinea* (*Lewis et al.* 1802) showing nyctinastic leaf movements.

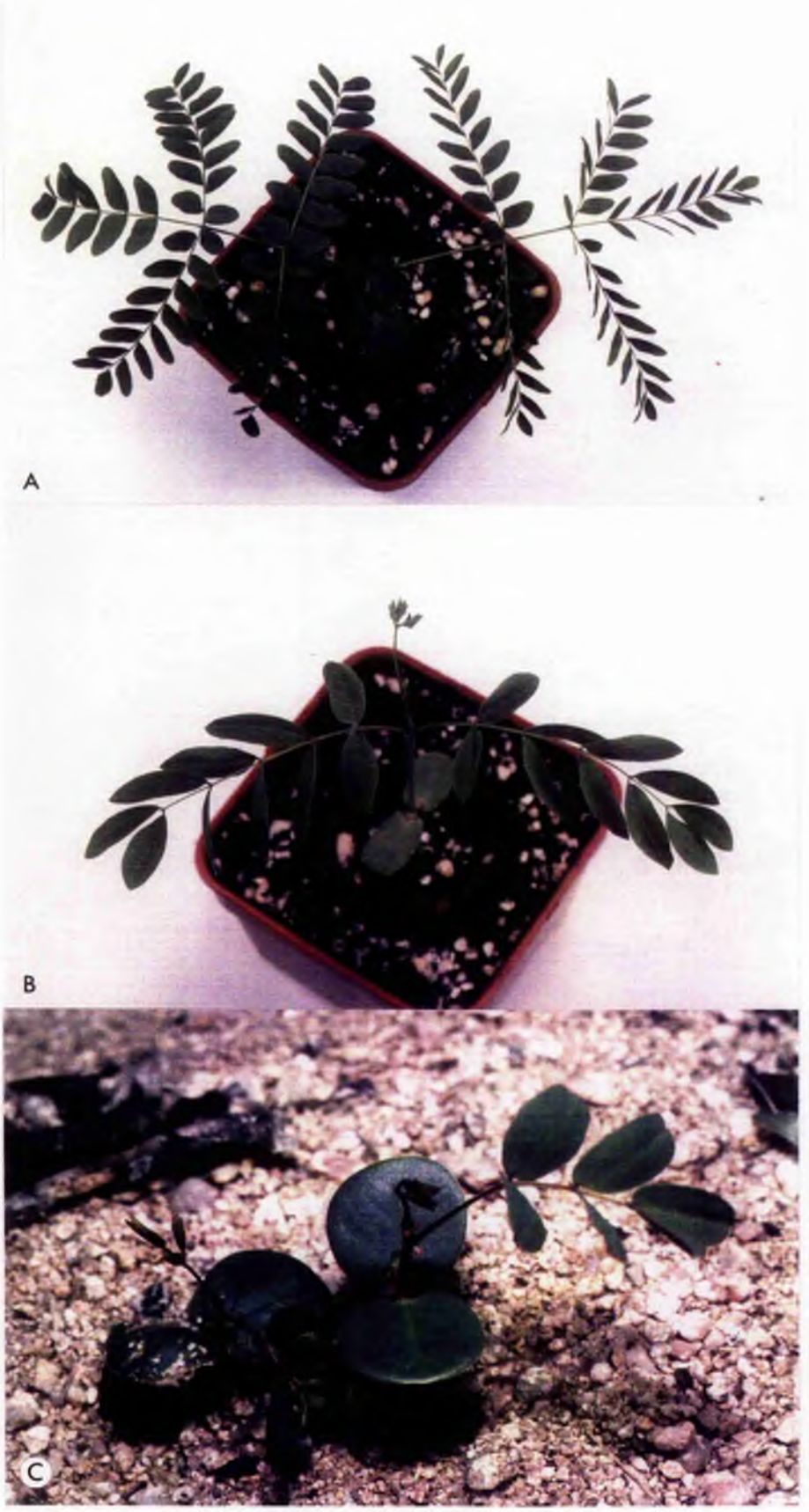


FIG. 11. Seedlings: **A** *C. eriostachys* (*Lewis & Hughes* 1799); **B** *C. pulcherrima* (*Lewis & Hughes* 1715); **C** *C. pannosa* (*Lewis et al.* 2033).

only partially so. The initial survey of nyctinasty in leaves of *Caesalpinia s.l.* suggests that a more detailed study would be taxonomically revealing.

SEED CHEMISTRY

Several authors have found and remarked upon the potential value of non-protein amino acids as taxonomic characters in the Leguminosae, either at the tribal, generic or subgeneric level (e.g. Bell, 1981). In the tribe Caesalpinieae surveys of non-protein amino acids in seeds have indicated that the distribution of compounds may provide useful characters for determining the limits of poorly-defined genera such as *Caesalpinia sens. lat.* (Evans and Bell, 1978; Watson and Fowden, 1973). The main classes of seed non-protein amino acids found in *Caesalpinia sens. lat.* are substituted glutamic acids, phenylalanines and pipecolic acids. Kite and Lewis (in press) in a cladistic analysis of these compounds in *Caesalpinia sens. lat.* have demonstrated certain correlations with macromorphological groupings of species and their data support a redefinition of *Caesalpinia sens. lat.* since many of the informal groups within it show closer chemical affinities with other genera than with other groups of *Caesalpinia sens. lat.* Kite and Lewis demonstrate a chemical relationship between the *Brasilettia* group of *Caesalpinia sens. lat.* and three species in the *Russellodendron* group: *C. cacalaco, C. spinosa* and *C. vesicaria*, due to the shared presence of substituted phenylalanines (Fig. 12C) and provide phytochemical support for the reinstatement of *Brasilettia* at generic rank. They also highlight a chemical divergence in the *Poincianella* group with only Mexican and Central American species in *Poincianella* A (together with *Haematoxylum brasiletto*) accumulating 4-methyleneglutamic acid. The Brazilian species of *Poincianella* B have quite a different profile of non-protein amino acids, since they apparently lack any substituted glutamic acids (Fig. 12D). This chemical difference between the geographically segregated parts of the group may have either taxonomic or ecological significance.

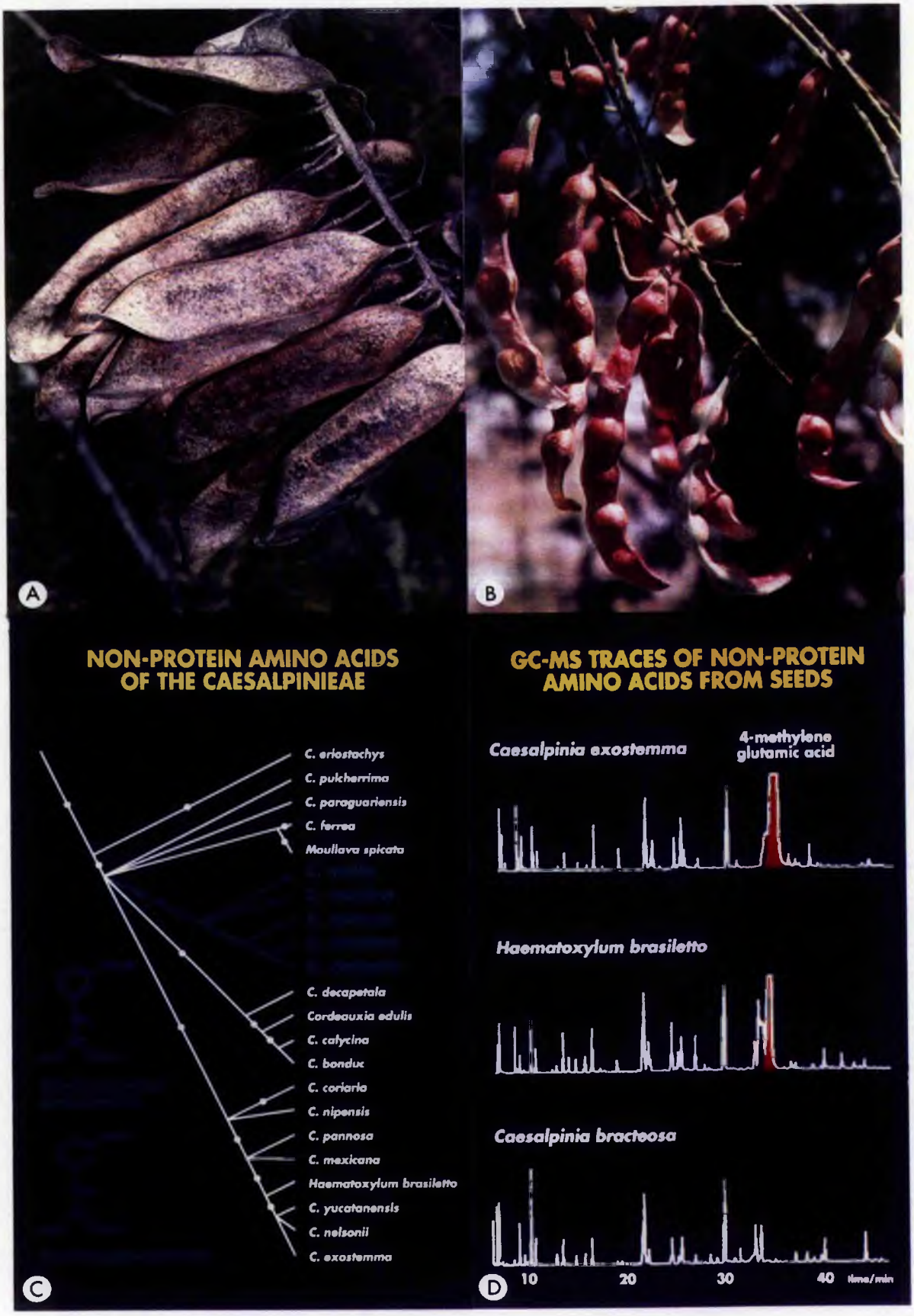


FIG. 12. **A** *Caesalpinia* (*Brasilettia*) *velutina* fruits (*Lewis & Hughes* 1714); **B** *C. (Russellodendron) cacalaco* fruits (*Lewis et al.* 1789); **C** chemical grouping of *Brasilettia* and *Russellodendron* groups; **D** chemical divergence of Central American/Mexican species (*Caesalpinia exostemma [Poincianella* A] and *Haematoxylum brasiletto*) and Brazilian species (*Caesalpinia bracteosa* [*Poincianella* B].

INSECTS

The bruchid *Stator sordidus* (Horn) was collected from seeds of *Caesalpinia eriostachys* and *C. hughesii* in Mexico by Lewis et al. (see Johnson and Lewis, 1993 and Fig. 13C). Some species of *Caesalpinia sens. lat.*, such as those mentioned above and *C. vesicaria* (*Russellodendron* group), seem very susceptible to bruchid attack while others appear to be extremely resistent (e.g. *C. cacalaco*, also in the *Russellodendron* group).

POLLEN

Graham and Barker (1981) reviewed surface structure of pollen in Caesalpinioideae and found several morphological groups in the tribe Caesalpinieae with a dominant type occurring in *Caesalpinia* and several other genera (*Cordeauxia, Haematoxylum, Hoffmannseggia, Mezoneuron, Pterolobium, Stuhlmannia* and *Zuccagnia*) of the '*Caesalpinia* group' of Polhill and Vidal (1981). This type consists of spherical, tricolporate grains with reticulate surfaces and a broad, granular-membraned margos (ridges) surrounding weakly developed colpi. Tsukada (1963) described the broad granular zone surrounding the apertures as a margocolpus. In *C. pulcherrima* and *C. gilliesii* apices of the margocolpus fuse (the grains are synmargocolpate) but in all other species of *Caesalpinia sens. lat.* examined to date the colpi do not fuse. Graham and Barker (loc. cit.) suggested that this feature might prove useful in separating *Caesalpinia* into subgroups and in detecting relationships between species but a wider survey of members of the *Caesalpinia* group by K. Hodivala (unpublished) revealed little of taxonomic significance. Most species conformed to the dominant type noted by Graham and Barker (1981).

The butterfly-pollinated *C. pulcherrima* has been reported to have 'viscin threads' (Cruden and Hermann-Parker, 1979) and these can be clearly observed in fresh condition holding the pollen together. These threads are also present in *Jacqueshuberia* (in the *Peltophorum* group of the Caesalpinieae). Because of the lack of free ends that would make the sporopollenin strands homologous to those of the Onagraceae, Patel *et al.* (1985) called these interpollen strands in the Caesalpinieae exine bridges.

Cocucci *et al.* (1992) found that the pollen of the moth-pollinated *C. gilliesii* is held together in clumps by a sticky 'pollen cement' which contains needle-like crystals. It would appear that the exine bridges of *C. pulcherrima* and the pollen cement of *C. gilliesii*

are related to pterotriby. The pollen becomes attached to the insects wings in sticky clumps. This compares with the 'dry' pollen of most *Caesalpinia sens. lat.* species which are pollinated by bees. It seems most likely that pollen structure in species of *Caesalpinia sens. lat.* is related to pollination systems and does not have phylogenetic implications at this level. It is predicted that *Caesalpinia* species pollinated by bees will not have exine connections.

CHROMOSOMES

Goldblatt (1981) postulated a base chromosome number of x = 14 in tribe Caesalpinieae but *Caesalpinia* and close relatives differ in having numbers of n = 12 (the number common and perhaps basal in the Detarieae-Amherstieae). Out of 24 species of *Caesalpinia* with known chromosome counts (Goldblatt, loc. cit.) all but two have 2n = 24. Goldblatt dismissed counts of 2n = 22 and n = 11 as errors in *C. pulcherrima* and *C. japonica* but saw no reason to doubt haploid numbers of n = 11 for *C. cucullatum* and *C. kavaiense* in subgenus *Mezoneuron*. Seven species of *Hoffmannseggia* (presumably *sensu lato*) were reported as having n = 12. My results, based on a limited survey of five species, uphold the findings of Goldblatt. *C. melanadenia, C. nelsonii, C. exostemma* and *C. hughesii* (in the *Poincianella* group) and *C. cacalaco* (in the *Russellodendron* group) all have n = 12.

Guerra (unpublished), working mainly on seed material sent from Kew, also found 2n = 24 to be the common number for *Caesalpinia sens. lat.* He confirmed my findings for *C. exostemma* and *C. cacalaco* and found the same number for *C. bonduc* (subgenus *Guilandina*), *C. velutina* (*Brasilettia* group), *C. vesicaria* (*Russellodendron* group), *C. gilliesii* (*Erythrostemon* group), *C. pulcherrima* (*Caesalpinia sens. strict.*), *C. yucatanensis* (*Poincianella* group) and *C. decapetala* (unplaced Old World species). He reports polyploidy in C. *ferrea* (*Libidibia* group) with 2n = 24, 48 and in *C. bracteosa* (*Poincianella* group), 2n = 48.

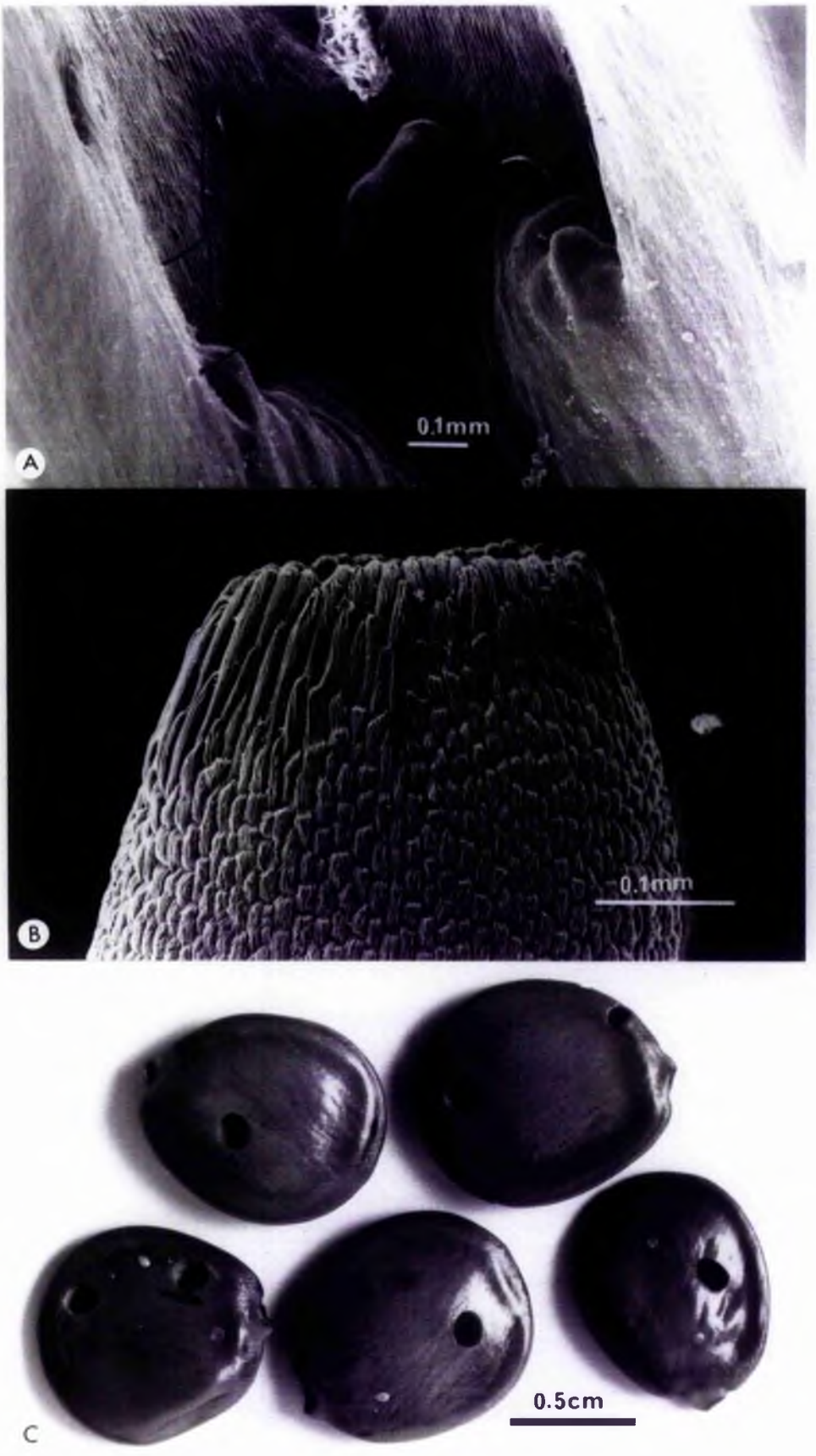


FIG. 13. *Caesalpinia exostemma* subsp. *exostemma* **A** appendage at apex of standard petal claw (*Lewis & Hughes* 1708); **B** stigma (*Lewis & Hughes* 1708); *C. hughesii:* **C** seeds with bruchid emergence holes (*Lewis et al.* 1795).

PHYLOGENY

As stated in the introduction, once broad morphological groups had been recognised within *Caesalpinia sens. lat.* a preliminary cladistic analysis of these and closely related genera, together forming the *Caesalpinia* group of Polhill and Vidal (1981),was carried out in an attempt to show evolutionary relationships between them. This work, under the title 'A reappraisal of the *Caesalpinia* group (Caesalpinioideae:Caesalpinieae) using phylogenetic analysis' has been accepted as a paper to appear in Advances in Legume Systematics, part 7 - Phylogeny, M.D. Crisp and J.J. Doyle (editors). B.D. Schrire co-authored the paper and it is included here as an integral part of the thesis rather than as an appendix. Where phylogeny figures 1-7 are referred to elsewhere in the thesis they include the word phylogeny to distinguish them from other figures with the same number.

ABSTRACT

A morphological cladistic analysis of the *Caesalpinia* group of Polhill & Vidal (1981) demonstrates that the traditional circumscription of the genus *Caesalpinia* is polyphyletic: some species are more closely related to other genera in the group than to each other. It is too early to reinstate genera presently in synonymy under *Caesalpinia sens. lat.* because all the species have not yet been analysed. The analysis does not, therefore, permit the delimitation of monophyletic groups. The placing of some species which are intermediate between higher taxonomic groups needs to be resolved before the exact number of genera in the *Caesalpinia* group can be determined. Taxa in the *Caesalpinia* group have distinct suites of defense organs; some have spines, prickles and lower calyx lobe cucullate in bud, others possess various types of glands and other secretory structures.

I. INTRODUCTION

"The Caesalpinieae is apparently a remarkable mixture of relics and complexes of relatively recent speciation, providing many pitfalls for formal systematics and biogeographical interpretations ... So many features that become fixed in more advanced groups of legumes are transitional and unstable in the Caesalpinieae" (Polhill & Vidal, 1981). It is not uncommon for individuals within a population of one species of *Caesalpinia* to have glandular or eglandular fruits, glandular or eglandular leaflets and

variable leaflet morphology which, in the absence of additional information, has caused several systematists to describe more than one species from herbarium specimens.

The tribe Caesalpinieae, as circumscribed by Polhill & Vidal (1981), contained about 410 species in 47 genera, placed in eight informal groups. The present study concentrates on the *Caesalpinia* group in which Polhill & Vidal (1981) placed 16 genera containing 176 species. Eight of the genera were monotypic, namely *Stahlia*, *Stuhlmannia*, *Lemuropisum*, *Wagatea* (= *Moullava*; see Nicolson, 1980), *Balsamocarpon*, *Zuccagnia*, *Stenodrepanum* and *Lophocarpinia*. Of the remaining eight, *Cordeauxia* had two species; *Conzattia* and *Haematoxylum* three each; *Cenostigma* six; *Pterolobium* 11; *Parkinsonia* (including *Cercidium*) 15; *Hoffmannseggia* 28 and *Caesalpinia* about 100. Based on unpublished data, *Stuhlmannia* is here considered to include *Cordeauxia* and *Caesalpinia insolita* (Harms) Brenan & Gillett (syn. *Caesalpinia dalei* Brenan & Gillett; see Capuron, 1967).

The *Caesalpinia* group cannot be understood without first unravelling the taxonomy of *Caesalpinia* sens. lat. This is a complex task because the genus is riddled with taxonomic misplacements and consequent nomenclatural confusion - twenty five generic names are currently in synonymy under *Caesalpinia*. This is largely due to the lack of a monographic treatment of *Caesalpinia* together with a tradition of trying to establish relationships between species based on rather superficial and fragmented revisions for regional floras. Britton & Rose (1930) displayed a sound knowledge of the North American taxa, and most of their genera approximate to groups of species in *Caesalpinia sens. lat.* discussed in the present analysis. They did describe, however, several monospecific genera based solely on fruit type, but in light of new data most of these can now be subsumed elsewhere in the *Caesalpinia* group.

The *Caesalpinia* group was distinguished from the *Peltophorum* group of Polhill & Vidal (1981) by having a modified lowermost sepal (which is sometimes cucullate); flowers generally zygomorphic with stamens crowded around the pistil at least towards the base; leaf axes adaxially ridged, at least distally to each insertion of leaflets (without specialised glands at the leaflet-insertions); and thorns, prickles, scattered glands and glandular hairs common. The present analysis followed the recommendations of Polhill & Vidal (1981) by giving more emphasis to flowers and defense systems in a world-wide

study of the *Caesalpinia* group and at the same time tested their hypothesis of two centres of diversity.

The type species of *Caesalpinia*, *C. brasiliensis* L., is quite unlike most species currently retained within *Caesalpinia sens. lat.* In this study *Caesalpinia sens. strict.* is represented by *Caesalpinia bahamensis* Lam. which is probably conspecific with *C. brasiliensis* or, at least, very closely related. The presence of scattered prickles and/or thorn-tipped woody bosses on main stems, petals shorter than sepals, a pronounced cucullate lower sepal, subepidermal glands present in petals and sometimes in sepals, and an open, funnel-shaped, fringed stigma link *Caesalpinia brasiliensis* with several species of *Mezoneuron*. The latter is presently recognised as a subgenus of *Caesalpinia* (Herendeen & Zarucchi, 1990) and extant species are unknown in the neotropics. Recently, however, Herendeen & Dilcher (1991) have shown that the *Mezoneuron* fruit-type was widespread in southern England and south-eastern North America in the Palaeocene-early Eocence. They suggest that this period was a phase of major diversification in the early evolution of the Caesalpinieae. The *Mezoneuron* fruit is generally a compressed, chartaceous legume with one margin winged and is usually indehiscent, but herbarium specimens show that there is a tendency for some fruits to open along the placental ridge, between fruit valve and wing. Within the *Caesalpinia* group no other taxa have exactly the *Mezoneuron* fruit-type but a trend towards this may be seen in species of *Haematoxylum* which have chartaceous fruits that dehisce along the middle of the valves. Variously shaped wings are found on the fruits of some other genera in the group but the overall fruit morphology of these genera are quite different to *Mezoneuron*. In this analysis the fruit wing character is simply coded as present or absent but in future the precise relationships between various states of this complex character need to be studied.

Haematoxylum, a genus adapted to xeric conditions, has two species in tropical America and the West Indies and one in Namibia. This phytogeographical pattern is not unusual within the Leguminosae and other similar distributions occur in the *Caesalpinia* group. *Parkinsonia* (including *Cercidium*) comprises about 15 species mostly in arid areas of central America and Mexico but one species occurs in South Africa and three in the horn of Africa. When *Hoffmannseggia*, as traditionally circumscribed, was scrutinized by the first author it became apparent that the African element revised by Brummitt & Ross

(1974) should be excluded. This African group, originally described as *Melanosticta* DC. (De Candolle, 1825) does,nevertheless, have affinities with the New World taxon *Pomaria*, which has species in southern USA and Mexico.

The genus *Pomaria* Cav. (1799) was reduced to a section of *Caesalpinia* by Bentham (1865) but it warrants detailed attention and might be reinstated at generic rank in the future. *Cladotrichium* Vogel (1837) from south-eastern Brazil and north-eastern Paraguay and Argentina is intermediate between *Pomaria* and *Melanosticta* and perhaps these three should be united. Burkart (1936) erroneously placed several Argentinian *Caesalpinia* species into section Pomaria, due to the presence of black glands on the leaflets, but they have closer affinities to *Caesalpinia* (*Erythrostemon*) *gilliesii*.

As pointed out by Polhill & Vidal (1981) many characteristics which have become fixed in "more advanced groups" are genetically plastic and unstable in the Caesalpinieae. An attempt has been made with collaborators to analyse as wide a range of characters as possible to construct a more robust dataset. Encouraging results are emerging from studies in floral ontogeny (Kantz and Tucker, Advances in Legume Systematics, part 6); floral gland anatomy (Rudall *et al.*, Advances in Legume Systematics, part 6); seed chemistry (Kite and Lewis, Advances in Legume Systematics, part 5); wood anatomy (Gasson, unpublished data); seed germination, seedling type and leaflet nyctinasty (Lewis and Simpson, unpublished) and chloroplast DNA restriction fragment pattern analysis (Simpson, in press).

II. METHODS AND MATERIALS

A. Terminal Taxa

Most of the taxa were studied from herbarium specimens at Kew. Several species of the genus *Caesalpinia* from Mexico, Central and South America were also studied in the field and grown in the greenhouse. Neotropical species of *Caesalpinia* were also studied from herbarium specimens on loan from A, BR, F, GH, HBG, M, MO, NY and US. So far, little detailed analysis has been undertaken by the authors on Old World taxa but revisions of *Caesalpinia* (including *Mezoneuron*) in Asia by Hattink (1974) and of *Pterolobium* by Vidal & Hul Thol (1974) provided useful data.

A total of 27 terminal taxa were included in the cladistic analysis (see Table I). In the larger genera, especially those principally from the Old World, not all species have yet been examined in detail, and one species was selected to represent each higher taxon. It should be noted that, in some cases, the character state assigned to the terminal taxon is not always ubiquitous in the higher taxon that it represents — e.g. *Hoffmannseggia glauca* has fruits with valves that do not twist (character 20), but several other species of *Hoffmannseggia* have valves that twist or even roll up. Some other genera and supraspecific taxa, also represented by a single species in this analysis, possess non-uniform characters. Precise distribution of these character states can only be established after further cladistic analysis at the species level. For *Caesalpinia sens. lat.*, species were selected to represent eight distinct species groups: *Caesalpinia sens. strict.*, *Brasilettia*, *Guilandina*, *Mezoneuron*, *Erythrostemon*, *Russellodendron*, *Libidibia* and *Poincianella*, all of which have been recognised at generic rank in the past. *Libidibia* and *Poincianella* are further divided into groups A and B based on the variability of characters displayed by species in each group. *Caesalpinia coriaria*, selected to represent *Libidibia* 'A' differs from *Caesalpinia ferrea* (*Libidibia* 'B') in characters 3, 5, 9 and 15 (see Table I). *Caesalpinia mexicana* (*Poincianella* 'A') differs from *Caesalpinia pyramidalis* (*Poincianella* 'B') in characters 5, 6, 10, 16 and 24. A total of 10 segregates are thus recognised within *Caesalpinia sens. lat.* On the cladogram the species representing each of these segregates is given the appropriate group name in parentheses e.g., *C.* (*Brasilettia*) *velutina*. It must be stressed, however, that reinstatement of these group names at generic rank, although implied, would at this time be premature. *Pomaria* (including *Melanosticta* and *Cladotrichium*) is scored separately from *Hoffmannseggia sens. strict.* but *Stuhlmannia* includes *Cordeauxia*. The terminal taxon *Haematoxylum* is coded to represent all species in the genus and the terminal taxon *Parkinsonia* to represent three species (see Table I). *Stahlia* is poorly-known in fruit and characters 19 and 22 have been scored as missing data. A comprehensive analysis, incorporating all the species of each genus in the *Caesalpinia* group, is an essential requirement before any new classification of the group can be proposed.

B. Outgroups

Since no phylogenetic hypothesis exists for taxa in the Caesalpinieae, outgroups were selected from taxa thought to be closely related to the *Caesalpinia* group by Polhill & Vidal (1981). The *Peltophorum* group of Polhill & Vidal (1981) shares with the *Caesalpinia* group the diagnostic character of introrse anther slits and the genus *Peltophorum* was selected as presumed sister taxon to the ingroup. There are a number of characters excluding *Peltophorum* from the *Caesalpinia* group, i.e., the genus has a peltate stigma (absent in the ingroup); the flowers are more or less regular and lack a differentiated lowermost sepal; the leaf rhachis is channelled and prickles, thorns or scattered glands are lacking. *Acrocarpus* was chosen as a second outgroup because Polhill & Vidal (1981) suggested it was an isolated genus possessing regular flowers with essentially undifferentiated petals and a short, grooved style terminating in a solid, minute stigmatic pad, characters considered to be plesiomorphic with reference to the ingroup.

C. Characters

The following 25 characters were used in the analysis (Table I). The multistate characters 0, 6, 10 and 14 were run non-additively. Our hypothesis is that the multistate characters 13, 17 and 18 have developed in the indicated sequence and these have therefore been treated additively in this analysis.

0. Habit: 0 = tree or shrub, 1 = climbing shrub or liana, 2 = herb.
1. Trunk and branch armature: 0 = unarmed, 1 = armed.
2. Stem glands (excluding pearl bodies) on younger stems: 0 = absent, 1 = present.
3. Leaf pinnation: 0 = terminating in a pair of pinnae, 1 = terminating in a single pinna (sometimes reduced to a single pinna).
4. Leaf rhachis upper side: 0 = channelled or ridged, 1 = terete (including ribbed and slightly flattened).

Table I. Data matrix used in the cladistic analysis of the Caesalpinia group.

Taxa	Characters																								
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
PELTOPHORUM dubium	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0
ACROCARPUS fraxinifolius	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0
CONZATTIA multiflora	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	1	0	0	0	0	1	1
PARKINSONIA *	0	1	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	1	1	0	0	1	0	0	1
LEMUROPISUM edule	0	0	0	1	0	0	2	0	0	0	2	0	1	2	2	1	0	1	2	0	0	1	0	0	1
Caes. (BRASILETTIA) velutina	0	0	0	0	1	0	1	1	0	0	1	0	1	2	2	0	0	1	2	1	0	1	0	0	0
CAESALPINIA (sens. strict.) bahamensis	0	1	0	0	1	0	1	1	0	0	0	0	1	2	1	1	0	1	2	0	1	1	0	1	1
Caes. (GUILANDINA) bonduc	1	1	0	0	1	0	1	1	0	0	0	0	0	2	2	0	0	1	3	0	0	1	0	0	0
Caes. (MEZONEURON) cucullata	1	1	0	0	1	0	1	1	0	0	0	0	1	2	1	1	0	1	1	1	0	0	0	1	1
PTEROLOBIUM stellatum	1	1	0	0	1	0	1	0	0	0	0	1	1	2	2	1	0	2	1	1	0	0	0	0	1
Caes. (ERYTHROSTEMON) gilliesii	0	0	1	1	1	1	1	1	1	0	0	0	1	2	2	1	0	1	2	0	1	1	0	0	1
STUHLMANNIA - all spp. **	0	0	1	0	1	1	2	1	1	0	2	0	1	2	2	0	0	2	2	0	0	1	0	0	0
HAEMATOXYLUM - all spp. ***	0	1	0	0	1	0	1	1	1	0	0	0	1	2	2	0	0	2	3	0	0	0	0	1	1
MOULLAVA spicata	0	1	0	0	1	0	1	1	0	0	0	0	1	2	1	0	1	2	1	1	0	1	0	0	1
Caes. (RUSSELLODENDRON) cacalaco	0	1	0	0	1	0	1	1	0	0	0	0	0	2	2	0	1	2	2	1	0	1	0	1	1
LOPHOCARPINIA aculeatifolia	0	1	0	1	1	0	1	1	0	0	1	0	0	2	2	1	1	2	2	1	0	0	0	0	1
Caes. (LIBIDIBIA 'B') ferrea	0	0	0	1	1	0	1	1	0	0	0	0	0	2	2	0	1	2	2	1	0	1	1	1	1
Caes. (LIBIDIBIA 'A') coriaria	0	0	0	0	1	1	1	1	0	1	0	0	0	2	2	1	1	2	2	1	0	1	1	1	1
STAHLIA monosperma	0	0	0	1	1	1	0	1	0	1	1	0	1	2	2	0	0	2	2	?	0	1	?	1	1
ZUCCAGNIA punctata	0	0	1	1	1	1	0	1	0	1	0	0	1	2	2	0	0	1	2	1	0	1	0	1	1
CENOSTIGMA macrophyllum	0	0	1	1	1	0	0	1	0	1	1	0	1	2	2	0	0	2	2	0	1	1	1	0	0
Caes. (POINCIANELLA 'A') mexicana	0	0	1	1	1	0	0	1	0	1	0	0	0	2	2	0	0	2	2	0	1	1	0	0	1
Caes. (POINCIANELLA 'B') pyramidalis	0	0	1	1	1	1	1	1	0	1	1	0	0	2	2	0	1	2	2	0	1	1	0	0	0
BALSAMOCARPON brevifolium	0	1	1	1	1	0	0	1	1	1	0	0	0	2	2	0	1	2	3	1	0	1	1	0	1
HOFFMANNSEGGIA (sens. strict.) glauca	2	0	1	1	1	0	0	1	1	1	2	0	0	2	2	0	1	2	3	0	0	1	0	0	1
STENODREPANUM bergii	2	0	1	1	1	1	0	1	1	1	0	0	1	2	2	0	1	2	3	0	0	1	0	1	1
Hoff. (POMARIA) jamesii	2	0	1	1	1	1	2	1	1	1	2	0	1	2	2	0	1	2	3	0	1	1	0	0	1

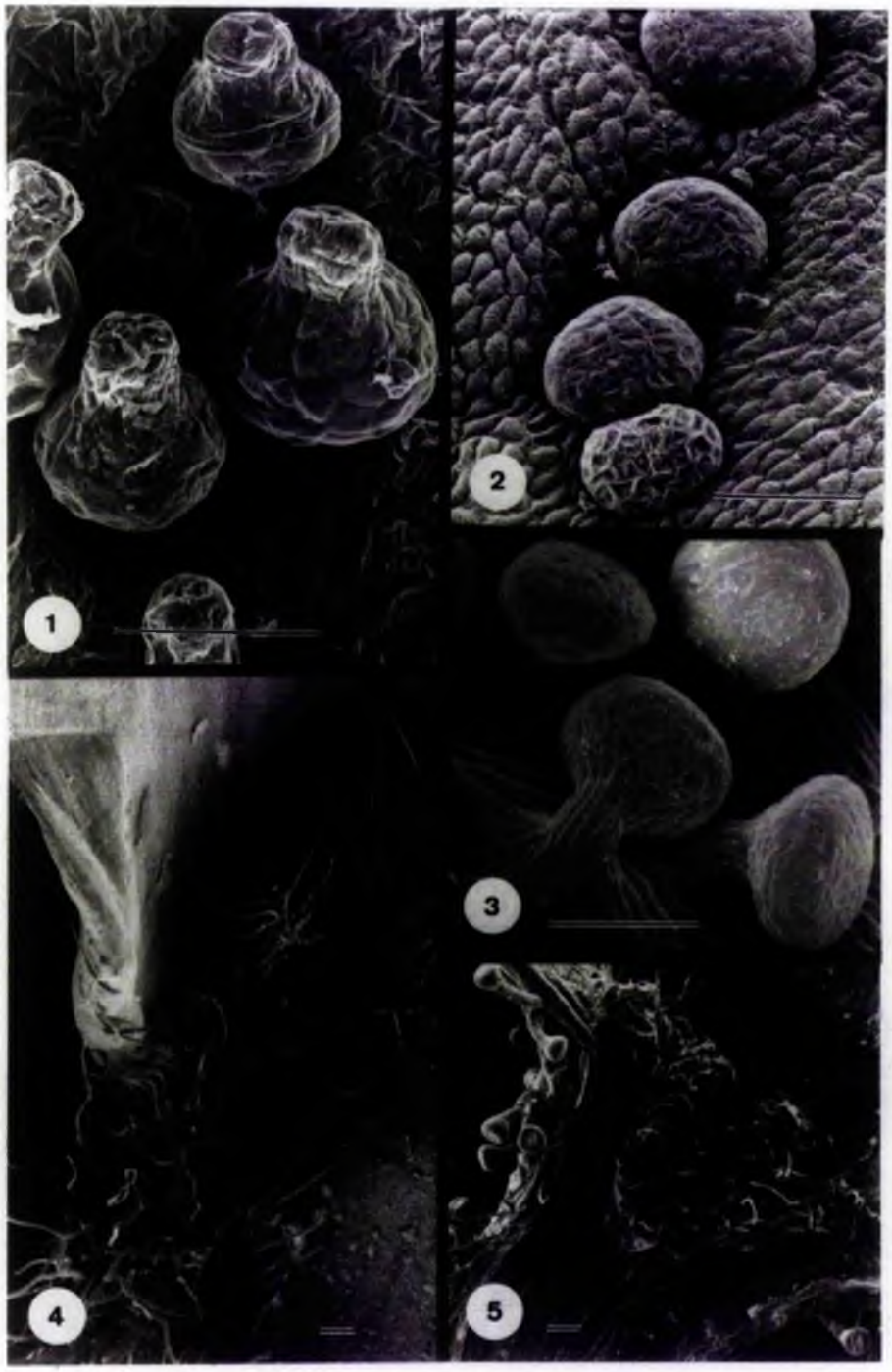
* includes P. aculeata, P. scioana and P. raimondoi

** includes Caesalpinia insolita and Cordeauxia edulis

*** i.e. H. brasiletto, H. campechianum and H. dinteri

5. Leaflet surface glands: 0 = absent, 1 = present (punctate to stalked).
6. Bud aestivation: 0 = imbricate, 1 = cucullate, 2 = valvate.
7. Calyx base: 0 = symmetrical, 1 = slightly asymmetrical to strongly gibbous.
8. Sepal surface glands: 0 = absent, 1 = present (Fig. 1).
9. Standard dorsal face: 0 = eglandular, 1 = glandular (Figs. 2 and 3).
10. Standard claw: 0 = absent or simple, 1 = folded or grooved, 2 = forming an inrolled tube.
11. Petals: 0 = heteromorphic, 1 = homomorphic.
12. Base of standard: 0 = with small tuft of hairs (Figs. 4 and 5), 1 = glabrous.
13. Stamen filaments: 0 = glabrous, 1 = with small tuft of hairs at base, 2 = hairy for at least $^1/_2$ to $^2/_3$ of length.
14. Stamen hairs: 0 = absent, 1 = rusty brown or reddish, 2 = white or hyaline.
15. Stamen length: 0 = about equalling petals or shorter, 1 = exserted from corolla.
16. Stigma position: 0 = terminal, 1 = sublateral (due to style curvature) or lateral.
17. Stigma type: 0 = solid, 1 = hollow funnel-shaped or flared, 2 = porate/ tubular.
18. Stigma rim: 0 = absent, 1 = present but unfringed, 2 = totally fringed, 3 = partially fringed.
19. Fruit dehiscence: 0 = dehiscent, 1 = indehiscent.
20. Fruit valves: 0 = untwisted, 1 = twisted.
21. Fruit wing: 0 = present, 1 = absent.
22. Hypanthium at fruit base: 0 = persisting as ring or cup, 1 = absent.
23. Sepal hairs (excluding margin): 0 = present, 1 = absent.
24. Sepal hair colour: 0 = rusty brown, 1 = hyaline or absent.

With the exception of characters 19 and 22 for *Stahlia* only characters for which information could be obtained for all the taxa were used in the analysis. This resulted in an apparent bias towards floral characters.



Figs. 1–5. Floral structures in the *Caesalpinia group*. 1. *Caesalpinia* (*Pomaria*) *ortegae* (Mexico: *Gentry 1641*), glands on calyx. 2. *Caesalpinia* (*Poincianella* A) *nelsonii* (Mexico: *Lewis et al. 1794*), sessile glands on upper dorsal surface of standard petal. 3. *Caesalpinia* (*Poincianella* A) *nelsonii* (Mexico: *Lewis et al. 1794*), stalked glands on lower dorsal surface of standard petal. 4. *Caesalpinia* (*Poincianella* A) *yucatanensis* (Guatemala: *Lewis & Hughes 1759*), hairs at base of standard petal blade. 5. *Caesalpinia* (*Poincianella* A) *epifanioi* (Mexico: *Contreras 1818*), tuft of hairs at base of standard blade. Scale bar = 0.1 mm.

D. Analyses

Cladograms were generated on an Amstrad 80286 microcomputer using HENNIG 86 (Farris, 1988). 465 equally parsimonious trees of length = 106 steps, ci = 0.31 and ri = 0.59 were produced, using the approximate algorithm (options mhennig* followed by bb*).

Poor resolution was obtained in the strict consensus tree (fig. 6) and successive weighting was applied to help choose among multiple equally parsimonious cladograms (Carpenter 1988). The first round of weighting produced a single tree 3 steps longer than the most parsimonious trees (when weights = 1), while subsequent iterations generated 15 trees, each 8 steps longer than the unweighted trees.

The selection of a cladogram, for discussion of characters, was based on finding the closest match of the single first-round weighted tree, with a topology among the original 465 trees. Since the longer weighted tree could not be matched precisely with the latter, nodes are marked with arrows on the cladogram (fig. 7) to indicate those also supported in the weighted tree.

The character analysis programme CLADOS (Nixon 1991) was used as an interactive tree editor to obtain diagnostic information on character distribution in the cladogram, and to optimise characters 8 and 10 using ACCTRAN. This interpretation of character evolution was favoured as being more consistent with other data.

III. RESULTS AND DISCUSSION

It is evident from the cladistic analysis that the genus *Caesalpinia*, as traditionally circumscribed, is polyphyletic. In none of the 465 trees were the subgroups of *Caesalpinia* included in a unique clade. Some species of *Caesalpinia* are more closely related to other genera in the *Caesalpinia* group than to other species of *Caesalpinia*, e.g., *C. pyramidalis* to *Cenostigma macrophyllum* and *C. cucullata* to *Pterolobium stellatum*. The *Caesalpinia* group of Polhill & Vidal (1981), the ingroup of this analysis, is diagnosed by three synapomorphies: stamen hairs white or hyaline (character 14), stigma rim present but unfringed (character 18) and sepal hairs hyaline or absent (character 24).

Within the ingroup the *Parkinsonia* clade is further diagnosed by three synapomorphies: stamen filaments hairy for at least half their length (character 13), stigma

FIG. 6 **STRICT CONSENSUS TREE FROM UNWEIGHTED ANALYSIS**

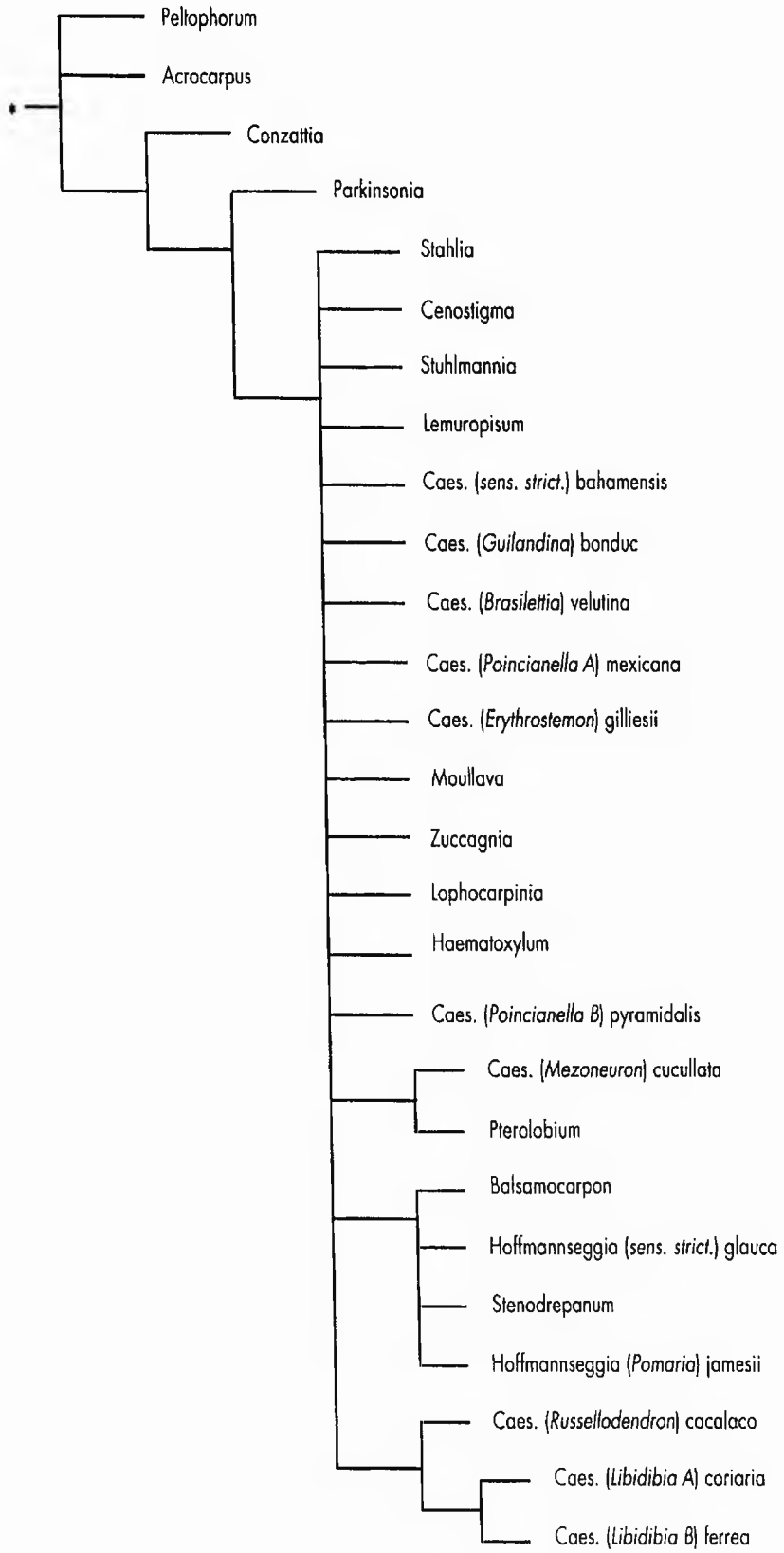
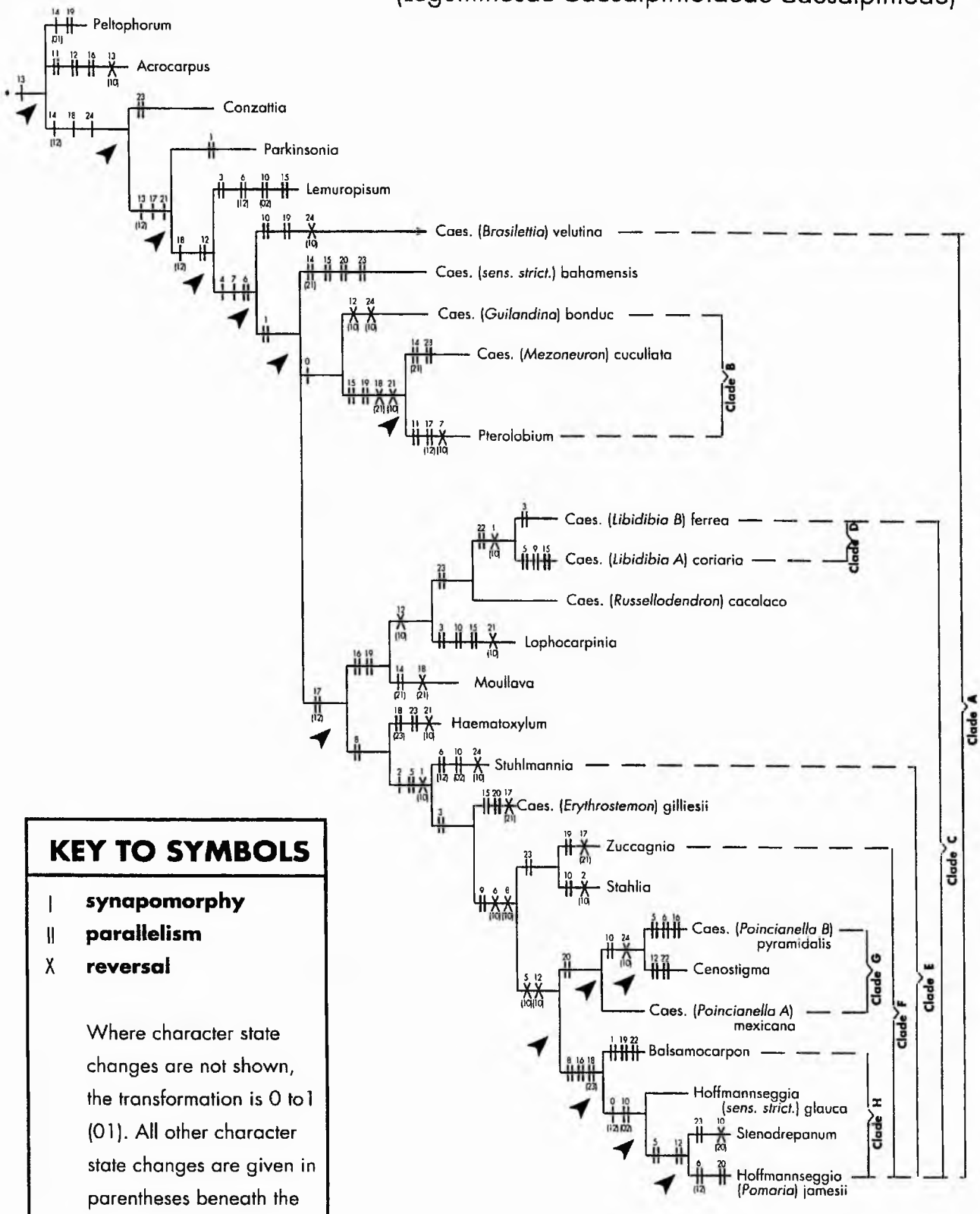


Fig. 7 **PRELIMINARY CLADOGRAM OF THE CAESALPINIA GROUP**

(Leguminosae-Caesalpinioideae-Caesalpinieae)



KEY TO SYMBOLS

|	**synapomorphy**
||	**parallelism**
X	**reversal**

Where character state changes are not shown, the transformation is 0 to1 (01). All other character state changes are given in parentheses beneath the symbol.

Nodes supported in the weighted tree

hollow funnel-shaped or flared (character 17) and fruit wing absent (character 21). The *Lemuropisum* clade is diagnosed by one synapomorphy, stigma rim totally fringed (character 18) and supported by one parallelism, standard base glabrous (character 12). The node above *Lemuropisum*, i.e. clade A (see Fig. 7), includes all segregates of *Caesalpinia sens. lat.* and their related genera. A further seven clades (B to H) are considered within Clade A. This basal clade of *Caesalpinia sen.lat.* is diagnosed by two synapomorphies: leaf rhachis terete (character 4) and calyx base asymmetrical (character 7), and supported by one parallelism, bud aestivation cucullate (character 6).

Clades B and C form an unresolved polytomy with *Caesalpinia bahamensis*,representing *Caesalpinia sens. strict.*, at the base. Clade B is diagnosed by one synapomorphy: the climbing habit (character 0) and includes three taxa: *Caesalpinia bonduc*, *Caesalpinia cucullata* and *Pterolobium stellatum*. *Caesalpinia bonduc* is a member of subgenus *Guilandina* (L.) Gillis & Proctor of *Caesalpinia* and *C. cucullata* is in subgenus *Mezoneuron* (Desf.) Vidal ex Herendeen & Zarucchi. Plants in this lineage, together with *Caesalpinia bahamensis*, are all armed with recurved prickles which assist in the climbing habit and presumably have a defense function as well. Within clade B, *C.* (*Mezoneuron*) *cucullata* and *Pterolobium stellatum* are united by two parallelisms: exserted stamens (character 15) and fruits indehiscent (character 19). This node is also supported by two reversals: presence of a fruit wing (character 21) and stigma rim present but unfringed (character 18).

Clade C is defined by the development of a porate/tubular stigma (character 17) which also occurs as a parallelism in *Pterolobium* (clade B) and includes 17 taxa, ten of which are currently recognised as distinct genera, six as species of *Caesalpinia sens. lat.* and one as a species of *Hoffmannseggia sens. lat.*, i.e., *H. jamesii*.

One lineage within clade C is defined by two parallelisms: stigma position sublateral or lateral (character 16) and fruit indehiscent (character 19) and includes five taxa. Clade D includes both *Libidibia* A and B, supported by one parallelism: hypanthium at fruit base absent (character 22) and one reversal: loss of stem armature (character 1). The cladogram does not support the segregation of two taxa within *Libidibia*.

The *Haematoxylum* lineage is defined by the development of sepal surface glands (character 8) which are lost at the node supporting clade F and regained in clade H. The *Stuhlmannia* group, clade E, is diagnosed by one synapomorphy: stem glands present on

younger stems (character 2) supported by one parallelism: leaflet glands present (character 5) and a reversal: loss of stem armature (character 1). The inclusive *Erythrostemon* clade is supported by the parallel development of leaves terminating in a single pinna (character 3).

Clade F is united by one parallelism: standard dorsal face glandular (character 9) and two reversals: buds imbricate (character 6) and a loss of sepal surface glands (character 8). Within this clade *Zuccagnia* and *Stahlia* are paired by the parallel loss of sepal hairs (character 23) while clades G and H are defined by two reversals: a loss of leaflet surface glands (character 5) and standard with a small tuft of hairs at its base (character 12).

Clade G, the *Poincianella* clade, contains *Caesalpinia mexicana*, which here represents the Mexican and Central American species of *Poincianella* group A of *Caesalpinia*, *Caesalpinia pyramidalis* representing the phytochemically distinct Brazilian species of *Poincianella* group B (see Kite and Lewis, Advances in Legume Systematics, part 5), and *Cenostigma macrophyllum* from northeastern Brazil. The parallelism defining this clade is twisting fruit valves (character 20). Within clade G the segregation of *Poincianella* into two groups, A and B, is supported by the cladogram.

Clade H contains four neotropical taxa, the monospecific genera *Balsamocarpon* and *Stenodrepanum* from South America, *Hoffmannseggia sens. strict.* (with c. 10 species in southern USA and Mexico and c. 15 in western South America), represented in the analysis by *H. glauca* - the type species of the genus - and *Hoffmannseggia jamesii*, chosen to represent the *Pomaria* group of *Hoffmannseggia sens. lat.* The clade is defined by three parallelisms: stigma partially fringed (character 18), stigma position lateral or sublateral (character 16) and sepal surface glands present (character 8). *Balsamocarpon* is a shrub but the other three taxa in clade H are herbs (defined by character 0). *Stenodrepanum* and *Pomaria* are further distinguished from *Hoffmannseggia sens. strict.* by the parallel developments of leaflet surface glands (character 5) and a glabrous standard base (character 12).

IV. TAXONOMIC DEDUCTIONS AND CONCLUSIONS

An important conclusion that can be drawn from the cladogram is that the genus *Caesalpinia*, as traditionally circumscribed, is polyphyletic. If all species currently

recognised in *Caesalpinia* are retained then some other genera in the *Caesalpinia* group should also be included in the genus. Conversely, if genera such as *Pterolobium* and *Cenostigma* are upheld, as we would suggest, then *Caesalpinia sens. lat.* should be divided into segregate genera and at least four would seem to be provisional candidates based on the strict concensus tree of the unweighted analysis (Fig. 6): *Mezoneuron*, *Russellodendron*, *Libidibia* and the remaining elements of *Caesalpinia*. Based on the preliminary cladogram (fig. 7) a further five candidates could also be considered: *Brasilettia*, *Guilandina*, *Erythrostemon*, *Poincianella* A and *Poincianella* B.

Clade A of this analysis includes all elements of *Caesalpinia sens. lat.* The three genera basal to clade A, namely *Lemuropisum*, *Parkinsonia* and *Conzattia* were all included in the *Caesalpinia* group of Polhill & Vidal (1981) but the group could, perhaps, be recircumscribed to include only clade A of this analysis. Three novel characters do not occur in taxa basal to clade A: leaf rhachis terete, calyx base asymmetrical and bud aestivation cucullate. The thickened cucullate lower calyx lobe and associated asymmetry of the flower bud affords a novel development of a floral defense mechanism.

Within clade A some general trends in character evolution are apparent. Clade B, for example, consists of taxa that have developed the climbing habit and armed branches. Clade C, characterised by a shift in stigma type to porate/tubular, probably related to the development of a novel breeding system, also has a loss of armature in most taxa. This is paralleled by a loss of the climbing habit and a trend towards the development of various glandular defenses on stems, sepals and leaflets; i.e. a shift from prickles to glands as defense organs.

In clade H, the *Hoffmannseggia* lineage is herbaceous, whereas most other taxa in clade A are woody shrubs, trees or lianas.

More data need to be gathered in the *Caesalpinia* group before any new classification can be formalised. The selection of the terminal taxa in this analysis was based on a detailed survey of the *Caesalpinia* group over the last few years. It must be stressed, however, that for some genera and infrageneric groups there remain many species to analyse in detail and it is not possible at this stage to discuss monophyletic groups. Thus, *Caesalpinia* subgenus *Mezoneuron* contains 25--30 species, subgenus *Guilandina* 12--15 species, the genus *Pterolobium* 11 species and *Hoffmannseggia* sens. strict. about 25

species, but only one species from each of these higher taxa is represented by the corresponding terminal taxon in this analysis.

To date, all systematic studies of the tribe Caesalpinieae and the genus *Caesalpinia* have not included nearly enough species. Any conclusions about trends of character evolution or relationships between taxa have been, at best, highly speculative. The present analysis has gone only part way to redress this deficiency. Future studies should attempt to include at least one species from each of the major groups of species within *Caesalpinia sens. lat.*: *Brasilettia*, *Guilandina*, *Caesalpinia sens. strict.*, *Mezoneuron*, *Erythrostemon*, *Russellodendron*, *Libidibia* and *Poincianella* groups A and B,and should also include species of *Hoffmannseggia sens. strict.* and its segregate *Pomaria*.

Many taxonomically important characters cannot be gleaned from herbarium specimens of species in the *Caesalpinia* group and a more comprehensive dataset than the one analysed in this paper can only be constructed by studying more species *in situ*. Valuable data is still to be gathered on tree architecture, bark type, resin production, seedling germination and leaflet nyctinasty. Important work remains to be done in the fields of floral ontogeny, floral gland anatomy, wood anatomy, and seed phytochemistry. Preliminary molecular studies by Simpson (pers. comm.,1992) are providing excellent supportive data for the segregation of *Caesalpinia sens. lat.* and this work continues.

The *Caesalpinia* group is a puzzle with numerous pieces missing. It is now clear that all previous solutions are inappropriate but the overall picture of relationships will not be revealed until more data have been gathered and all species analysed.

BIOGEOGRAPHY

Most species of the *Poincianella-Erythrostemon* group grow in semi arid areas and are usually restricted to thorn scrub (including various forms of Brazilian caatinga vegetation) or open deciduous forest, either on sandy or calcareous soils. Some (e.g. *C. standleyi*) are known principally from highly degraded sites where seeds released by explosive fruit dehiscence result in rapid colonization of these open habitats. Many species have a preference for coastal habitats and most do not grow at altitudes above 1100 m but there are exceptions in both North and South America. *C. nicaraguensis*, a narrowly restricted endemic in central Nicaragua, grows in oak or mixed pine and oak forest between 1100-1400 m; *C. laxa* in eastern Mexico is known from 1400-2000 m and *C.*

fimbriata in western South America grows in semi arid thorn scrub at altitudes of 1300-3200 m. A few species in the group occupy more humid habitats, e.g. *C. pluviosa* var. *cabraliana* and the most widespread variant of *C. echinata* grow in moist coastal forests of eastern Brazil.

The *Poincianella-Erythrostemon* group has four main areas of species diversity:

1. **Mexico (including south eastern USA) and Central America**

Only *C. eriostachys* grows as far south as Panama (Map 9) and is by far the most widespread species in North America. Most species in Mexico are restricted to the lowlands of the Pacific and Gulf coasts (including the Yucatan Peninsula, Maps 12 and 13) but a group of closely related species are endemic to the dry valleys of the Rios Balsas Depression of Guerrero, Puebla and Michoacan (Map 7). *C. placida* and *C. pannosa* are endemic to Baja California (Maps 4 and 5) and three species are restricted to the arid north west of Mexico with *C. caladenia* known only from a small area of the Sonoran desert (Map 5). Species are lacking from the central mountains and deserts north of 20°N latitude although *C. sessilifolia* (in *Caesalpinia sens. strict.*, and thus excluded from this revision) is endemic to the Chihuahua desert.

2. **Cuba and Hispaniola**, with three endemic species in Cuba (Map 14), one in Hispaniola (Map 15) and *C. glandulosa* occurring on both islands (Map 15).

3. **N.E. Brazil**, with several species (Maps 16-19) occurring as dominants in the semi arid caatinga vegetation.

4. **West central South America** (Maps 20-22) including northern Argentina, central Bolivia, central Paraguay (east of the Paraguay river) and western Mato Grosso do Sul (in Brazil).

Species of *Poincianella* mainly occur in area 1-3 with only *C. marginata* and *C. pluviosa* var. *pluviosa* (Map 22) being found in area 4. Most *Erythrostemon* species, on the other hand, occur in area 4 with only *C. placida* (area 1, Map 5) and *C. calycina* (area 3, Map 17) as exceptions.

C. gaumeri from the Yucatan Peninsula of Mexico and western Cuba (Map 13) appears closely related to several species in NE Brazil, e.g. *C. laxiflora* (Map 19).

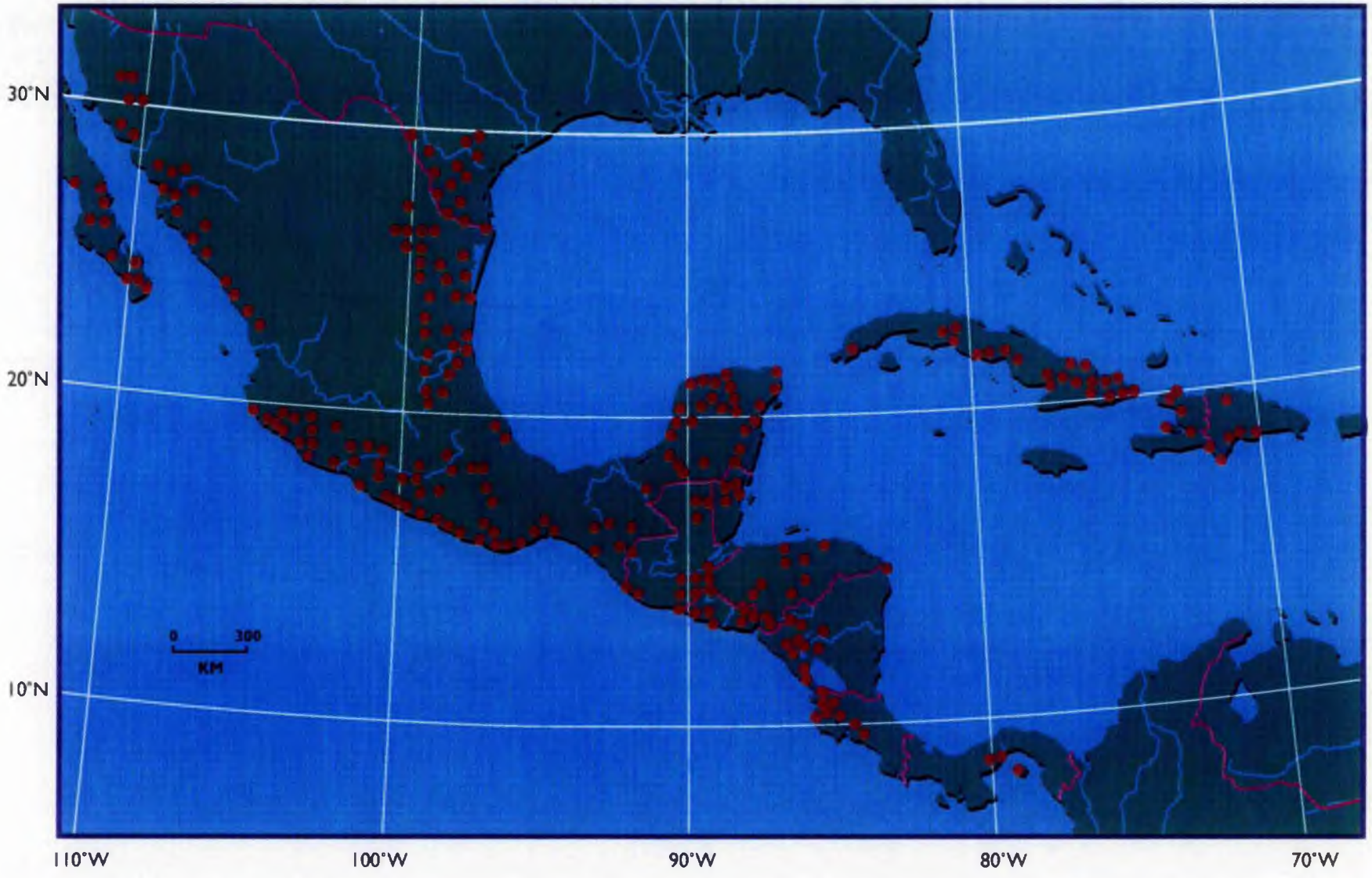
C. eriostachys (Map 9) has many of the characters of *C. pluviosa*, a species widespread in Brazil (Maps 18 and 22).

Maps 1 and 2 show the distribution of all 47 species (56 taxa) of the *Poincianella-Erythrostemon* group included in this revision. Although some gaps are undoubtedly due to under-collecting the lack of species in Ecuador, Colombia, Venezuela and the Guianas is noteworthy. Other groups of *Caesalpinia sens. lat.* do, however, grow in those countries, e.g. *Brasilettia* in Venezuela, *Russellodendron* in Ecuador and *C. cassioides* (*Caesalpinia sens. strict.*) (Fig. 72) in Columbia.

The majority of species in the *Poincianella-Erythrostemon* group fit the neotropical seasonal forests pattern of Prado (1991). There is a discontinuous extension of deciduous and semi deciduous forests from Mexico to Argentina occurring at low and middle altitudes. These have a strongly seasonal climate with a well defined dry season of variable length and are usually on mineral rich soils. In South America the overall pattern of *Poincianella- Erythrostemon* species fits the 'pleistocenic arc' of Prado and Gibbs (1993) and there is a close resemblance between their distribution map of *Anadenanthera colubrina* var. *colubrina* and var. *cebil* (Leguminosae-Mimosoideae) (Prado and Gibbs, 1993, fig. 2A) and the distribution pattern seen in Map 1 of this work. In both cases the species essentially avoid the Amazonian region and the cerrados of central Brazil. *C. pluviosa* var. *paraensis* (Map 18) is an exception found growing in open sandy areas around Monte Alegre in Pará state, Brazil. *Caesalpinia pyramidalis* (Map 16) closely fits one of the 'peculiar distributional patterns' discussed by Prado (1991). *C. pyramidalis* var. *pyramidalis* is a north east Brazilian (Bahia,Alagoas, Pernambuco) caatinga species while *C. pyramidalis* var. *diversifolia* is recorded from Ceará, Maranhão and Amazonas (close to Manaus).

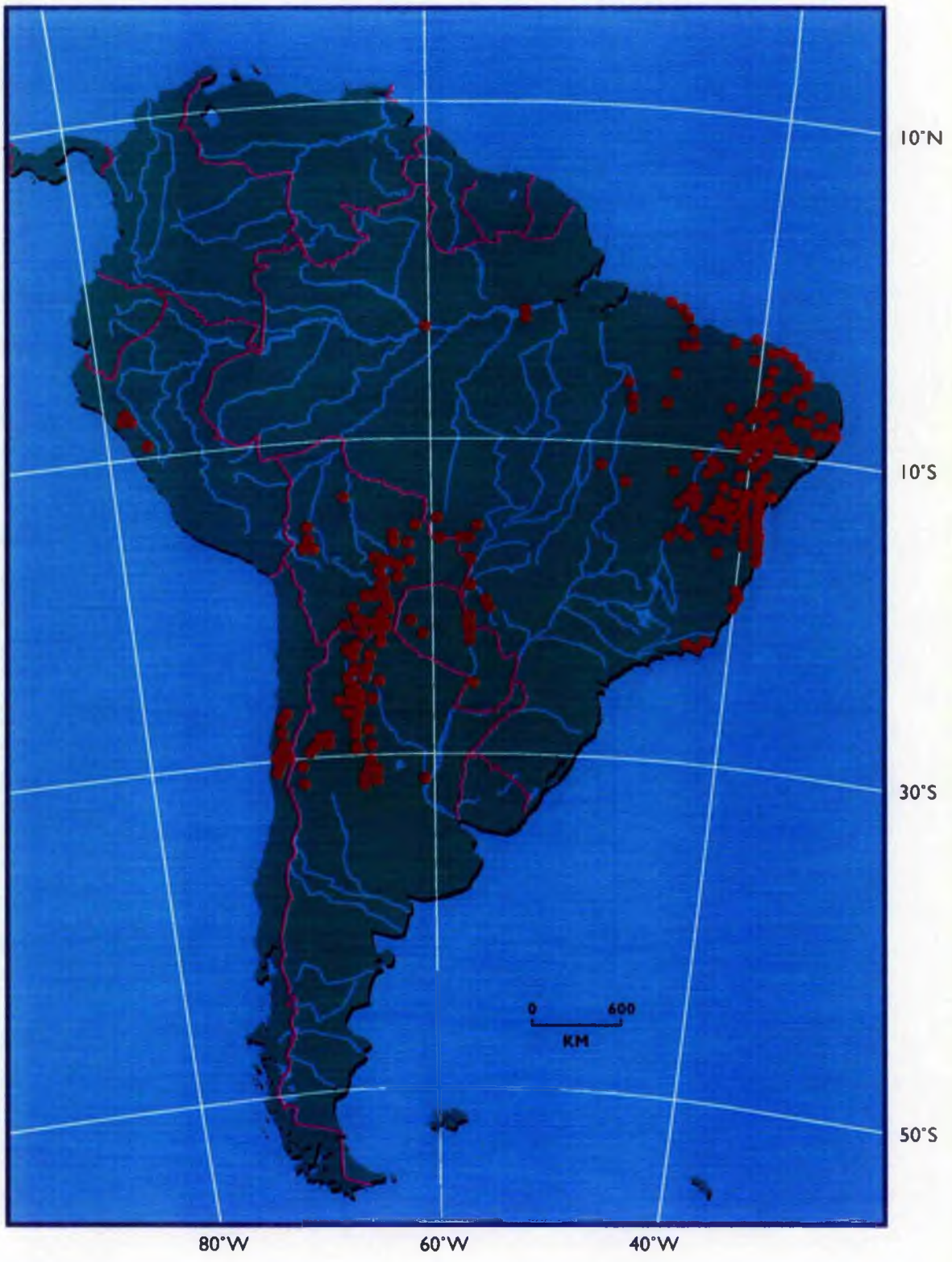
Lavin and Luckow (1993) discussed in detail the boreotropics hypothesis of Wolfe and Tiffney (Wolfe 1975,Tiffney 1985a, b) in relation to the distribution patterns seen in the *Dichrostachys* group of the Mimoseae (Leguminosae-Mimosoideae) and tribe Robineae (Leguminosae-Papilionoideae). The hypothesis suggests that biotas including presently North American lineages were once more widespread in the northern hemisphere and crossed the North Atlantic by direct land connections or over limited water gaps until the late Eocene or early Oligocene (Wolfe, l.c., Tiffney, l.c.). They noted that tropical fossil taxa shared by the early Tertiary fossil floras of North America and Europe were most closely related to extanct species in Asia and to some extent Central American and the Greater Antilles. This pattern is closely matched by the extant distribution of *Caesalpinia*

Distribution of the *Poincianella* - *Erythrostemon* group of *Caesalpinia* (●) in Mexico, Central America and the Caribbean



Map 1

Distribution of the *Poincianella - Erythrostemon* group of *Caesalpinia* (●) in South America



subgenus *Mezoneuron* (most diverse in Asia but with a few disjunct taxa in Africa and Madagascar) together with fossil evidence for *Mezoneuron* fruit types in south eastern USA and Europe (Herendeen and Dilcher, 1991). *Caesalpinia* subgenus *Mezoneuron* has no extant taxa in the neotropics. Other groups considered to be basal in *Caesalpinia sens. lat.* have a paucity of species in South America, e.g. *C. cassioides* (in Peru and Colombia) is the only native species of *Caesalpinia sens. strict.* in South America, and with the exception of *Caesalpinia mollis* in Venezuela all other species of the *Brasilettia* group are restricted to Central America and Mexico.

I predict that, after a detailed survey of Old World species of *Caesalpinia sens. lat.*, South America will be shown to contain only the more derived lineages of the genus and that the overall distribution pattern will fit well the boreotropical hypothesis.

FLORAL BIOLOGY

The flowers of most species of *Caesalpinia sens. lat.* are some of the more specialised in subfamily Caesalpinioideae. The secretory structures on the inner surface of the calyx tube produce abundant nectar which is retained within the calyx and protected by interlocking hairs at the bases of the ten stamens. Nectar is generally not easily accessible to non-specialised flower visitors. Kay (1987), based on observations by Jones and Buchman (1974), reported that only the 'flag' or standard petal of *C. eriostachys* is UV-absorbing (insect-red) with the four lateral petals being UV-reflecting (insect-purple). The stamen filaments are UV-reflecting and the anthers UV-absorbing. Visiting bees were seen to orientate themselves so that their head was towards the UV-absorbing standard. This guide mark is a conspicuous and important feature of yellow, zygomorphic, mellitophilous flowers in the Caesalpinioideae and Papilionoideae (Kay, loc. cit.). Differences in the UV patterning have been shown to contribute to the reproductive barriers between yellow-flowered species of *Cercidium* (Jones, 1978) and it is to be expected that similar barriers are operating in closely related, sympatric, yellow-flowered species of *Caesalpinia*. Appendix 2 examines the breeding systems of two north east Brazilian species of the *Poincianella-Erythrostemon* group.

TAXONOMY

A REVISION OF THE *POINCIANELLA-ERYTHROSTEMON* GROUP

A note on species descriptions and specimen citations

In the species descriptions, median leaflets are those in mid positions along a pinna rhachis which itself is in a mid position along the leaf rhachis. Flower pedicels are considered as the stalk from the calyx base to the point of attachment on the inflorescence rhachis. The pedicel is usually articulated at some point along its length in the *Poincianella-Erythrostemon* group. Each flower has five petals: the standard, the two upper laterals and the two lower laterals. Petal length includes the petal claw (if present), petal width is measured across the broadest part of the petal blade.

For each species, specimens are cited from north to south within their geographical range. Within each country, province or state specimens are subsequently cited alphabetically by collector's name. Herbarium acronyms cited in the text are those used in Index Herbariorum, eighth edition (Holmgren *et al.*, 1990).

References to the main black and white figures are in **boldface**.

Key to Species

1. Leaves consistently once pinnate..... 2
1. Leaves bipinnate..... 3
2. Leaflet lower surface with scattered subepidermal glands over blade surface and along margin, marginal or submarginal vein lacking, terminal leaflets of each pinna up to 3.5 x 2.6 cm, endemic to Cuba ..... 22. **C. pinnata**
2. Leaflet lower surface with glands along margin only, marginal or submarginal vein prominent, terminal leaflets 5--7.5 x 3--4.5 cm, Bolivia, western Brazil and northern Paraguay..... 27. **C. marginata**
3. Leaflets alternate on most pinnae of each leaf (occasionally opposite on the terminal pinna) 4
3. Leaflets opposite on all pinnae of each leaf 20

4. Young branchlets armed with upturned thorns arising from woody protuberances, fruits armed with woody spines, sepals roll inwards post anthesis, standard petal with a deep carmine central blotch, Brazil ..... 34. **C. echinata**

4. Plant unarmed, fruit without spines or prickles, sepals usually reflexed but not inrolled 5

5. Plants of Mexico, Central America, Cuba and Hispaniola 6

5. Plants of Brazil, Bolivia, Paraguay and Argentina 9

6. Pinnae in 1--4 opposite to alternate pairs, plus a terminal pinna (or this occasionally lacking) 7

6. Pinnae in 5--10 opposite to alternate pairs, plus a terminal pinna (or this lacking) 8

7. Trees, 4--20 m tall, fruits 6.7--10 x 2.2 cm, widest near the apex, Yucatan Peninsula (including Belize) and western Cuba .....21. **C. gaumeri**

7. Shrubs, 1--4 m tall, fruits up to 3.8 x 1.5 cm, widest at the middle, endemic to Cuba.....23. **C. myabensis**

8. Inflorescence with a ferrugineous-tomentose stellate indumentum, leaflet apices rounded to obtuse, fruits over 7 x 1.6 cm, widespread in Mexico and Central America but unknown in Hispaniola..... .....20. **C. eriostachys**

8. Inflorescence lacking ferrugineous stellate indumentum, apices of at least some leaflets of most leaves shortly apiculate, fruits up to 7 x1.7 cm, endemic to Haiti and the Dominican Republic..... 24. **C. pellucida**

9. Inflorescence rhachis and pedicels densely glandular, leaflets up to 1 x 0.7 cm (usually much smaller), leaves with 3--10 pairs of pinnae (plus a terminal pinna), pinnae with 11--21(--22) leaflets, Piauí, Pernambuco and northern Bahia .....32. **C. microphylla**

9. Inflorescence rhachis and pedicels eglandular or if a few glands intermixed with the indumentum then the leaflets over 1.5 x 1 cm 10

10. Leaves with 1--3 pairs of pinnae (plus a terminal pinna or this lacking), each pinna with (2--)3--13 leaflets, terminal leaflets of each pinna 1.7--8 x 1--7 cm..... 11

10. Leaves with 2--11 pairs of pinnae (plus a terminal pinna or this lacking), each pinna with 9--29(--31) leaflets 15
11. Pedicels articulated 10--12 mm below calyx (i.e. below middle), bracts ovate-lanceolate, acute to acuminate, c 3--3.5 mm long, standard claw apex with a glandular ridge, Pernambuco, Alagoas and Bahia..... ..... 28a. **C. pyramidalis** var. **pyramidalis**
11. Pedicels articulated directly below to 4.5 mm below calyx (i.e. above middle)..... 12
12. Bracts broadly ovate, acute, 8--12 mm long, flowers larger, the lateral petals 15--17 mm long..... .....29. **C. bracteosa**
12. Bracts lanceolate-ovate, acute to acuminate, 2.5--6 mm long, flowers smaller, the lateral petals 9--14 mm long..... 13
13. Flowers in lax racemes, inflorescence finely puberulous with whitish hairs, often with a few red glands intermixed, glabrescent..... 31. **C. laxiflora**
13. Flowers in compact pyramidal racemes or congested panicles, inflorescence densely rusty brown or yellowish-brown tomentose, eglandular..... 14
14. Terminal leaflets of each pinna 4--5.6 cm long, bracts 4.5--6 mm long, Amazonas, Maranhão and Ceará.....28b. **C. pyramidalis** var. **diversifolia**
14. Terminal leaflets 1.7--4.2 cm long, bracts 2.5--4 mm long, Piauí, Ceará, Rio Grande do Norte, Paraiba and Pernambuco ..... 30. **C. gardneriana**
15. Flowers in racemes 16
15. Flowers in panicles 17
16. Pinnae in 6--11 pairs per leaf (plus a terminal pinna), leaflets 19--31 per ..... pinna, stamen filaments 10--12 mm long..... .....33c. **C. pluviosa** var. **peltophoroides**
16. Pinnae in 4--6 pairs per leaf (plus a terminal pinna), leaflets 13--20 per pinna, stamen filaments 7--10 mm long .....33b. **C. pluviosa** var. **intermedia**
17. Leaflets 9--17 per pinna..... 18
17. Leaflets 18--29 per pinna 19
18. Stamen filaments 15--17 mm long, inflorescence indumentum yellowish-grey, central Bahia and northern Minas Gerais in the São Francisco valley..... ..... 33f. **C. pluviosa** var. **sanfranciscana**

18. Stamen filaments c. 10 mm long, inflorescence indumentum rusty brown, south eastern Bahia and north eastern Minas Gerais, and disjunct in Pará (around Monte Alegre) and Rio de Janeiro (around Cabo Frio)..... 33e. **C. pluviosa** var. **paraensis**
19. Leaflets shiny, fruit with black dashes scattered over valve surface, restricted to region around Santa Cruz Cabralia in south eastern Bahia..... ..... 33d. **C. pluviosa** var. **cabraliana**
19. Leaflets dull, fruit lacking black dashes, widespread in western Brazil, Bolivia, northern Argentina and Paraguay..... 33a. **C. pluviosa** var. **pluviosa**
20. Plant armed with woody prickles, Hispaniola and Cuba..... ... 26. **C. glandulosa**
20. Plant unarmed 21
21. Leaves terminating in a pair of pinnae, ovary two-ovulate, inflorescence pseudo-lateral, endemic to eastern Cuba..... 25. **C. nipensis**
21. Leaves terminating in a single pinna 22
22. Terminal pinna distinctly longer than the laterals, terminal pinna with 8--20 pairs of leaflets, laterals with 3--7 pairs, secondary venation of leaflets essentially palmate, dark punctate glands scattered over lower surface of leaflet lamina, southern U.S.A. (Texas and ? New Mexico) and northern Mexico (Nuevo Leon and Tamaulipas)..... ..... 47. **C. caudata**
22. Terminal pinna ± equalling or shorter than laterals and without a marked increase in leaflet number, secondary venation not palmate..... 23
23. Plants of Mexico or Central America 24
23. Plants of South America 55
24. Leaflets epunctate, lacking sessile glands on the blade or margin 25
24. Leaflets with dark punctate glands along part or all of the margin and sometimes also on the blade surface..... 47
25. Flowers laterally compressed (this apparent on herbarium specimens as well as in the field), standard petal with a central red blotch, stamens deflexed 26
25. Flowers not laterally compressed, standard petal with or without orange or reddish dots or veins but never with a central red blotch 28
26. Stamens c. twice the length of the petals, lateral petal claws eglandular, standard claw apex with a thickened, glabrous appendage..... ..... 10a. **C. exostemma** subsp. **exostemma**

26. Stamens but a little longer than petals, lateral petal claws stipitate-glandular.....27
27. Stamen filaments 13--16 mm long, pinkish-red (at least the apical ½), standard claw lacks apical appendage, Mexico (Vera Cruz and Tamaulipas)..... ..... 10b. **C. exostemma** subsp. **tampicoana**
27. Stamen filaments 20--24 mm long, greenish, standard claw apex with a pubescent (sometimes dentate) ridge, Mexico (Colima, Michoacan, Guerrero and Oaxaca)..... ..... 11. **C. hughesii**
28. Apex of standard claw (at junction with blade) lacks appendage or ridge (i.e. is plane) 29
28. Apex of standard claw (at junction with blade) with a thickened appendage or ridged 34
29. Stamens c. twice the length of the petals, inflorescence rhachis and pedicels glabrous, eglandular, standard up to 8 mm long with stipitate glands at base of dorsal surface, Mexico (Guerrero and Oaxaca).....15. **C. laxa**
29. Stamens equalling, to but a little longer than, petals.....30
30. Leaflets regularly orbicular-elliptic, up to 11 x 7 mm, petal blades essentially eglandular (a few glands on margin near base), plants 30--80 cm tall with rhizomatous, colony forming habit, base of calyx and apex of pedicel stipitate-glandular, inflorescence otherwise eglandular, legume suborbicular, 1--2-seeded, stamens 9--10 mm long, USA (south-eastern Texas) and Mexico (Tamaulipas) .....2. **phyllanthoides**
30. Leaflets generally obovate-elliptic to oblong- elliptic, petal blades glandular on dorsal surface (at least on basal half), low shrubs or small trees, 1--6 m tall (rarely smaller and prostrate) not rhizomatous nor colony forming, inflorescence rhachis and pedicels eglandular or densely glandular, stamens 10--13 mm long.....31
31. Inflorescence rhachis densely glandular, endemic to Baja California... 4. **C. pannosa**
31. Inflorescence rhachis eglandular 32
32. Leaflets fleshy, the secondary venation obscure or lacking, dorsal surfaces of petals densely red glandular, endemic to Baja California.....4. **C. pannosa**
32. Leaflets chartaceous, secondary venation ± prominent, brochidodromous, dorsal surfaces of petals yellow glandular 33

33. Pinnae in 2--4(--5) pairs per leaf (plus a terminal pinna), leaflets in (2--)3--5 pairs per pinna, widespread through central and eastern Mexico and into southern Texas .. ..1. **C. mexicana**

33. Pinnae in 1--2 pairs per leaf (plus a terminal pinna), leaflets in 2--3 pairs per pinna, Mexico (Jalisco)..... 3. **P. robinsoniana**

34. Petals salmon-pink or pinkish red 35

34. Petals yellow, the standard often with orange-red markings.....36

35. Inflorescence rhachis and pedicels densely stipitate-glandular, racemes 10--20-flowered arising from short woody brachyblasts, standard petal blade broadly triangular-hastate, pinnae in 1--2 pairs per leaf (plus a terminal pinna), leaflets in 3--4 pairs per pinna, stamen filaments 13--15 mm long, Mexico (Puebla and Oaxaca)..... 19. **C. melanadenia**

35. Inflorescence rhachis eglandular (pedicels occasionally densely stipitate-glandular), racemes multi-flowered, lax, erect or pendent, standard petal blade ovate, pinnae in 3--6 pairs per leaf (plus a terminal pinna), leaflets in (3--)4--6(--10) pairs per pinna, stamen filaments 6.5--11 mm long, Mexico (Puebla, Michoacan and Guerrero)..... ..... 16. **C. hintonii**

36. Leaflets in 5--7 pairs per pinna, terminal leaflets up to 18 x 10 mm, inflorescence densely golden tomentulose with golden-brown stellate or plumose hairs intermixed, standard claw ridge pubescent, stamens 16--17 mm long, endemic to Nicaragua..... 14. **C. nicaraguensis**

36. Leaflets in 2--5 pairs per pinna.....37

37. Inflorescence rhachis and pedicels densely stipitate-glandular with pixie-cup glands 38

37. Inflorescence rhachis and pedicels eglandular or at most with a few sessile or short-stalked mushroom-shaped glands intermixed.....39

38. Ridge at apex of standard claw densely pubescent, bracts larger, 6--11 mm long, terminal leaflets 10--25 x 5--15 mm, Mexico (Sonora)..... 8. **C. caladenia**

38. Ridge at apex of standard claw ± glabrous, bracts smaller, 4.5--7 mm long, terminal leaflets 18--44 x 14--25 mm, Mexico (Jalisco, Colima, Michoacan and Guerrero).....7. **C. acapulcensis**

39. Pedicels articulated (3--)5--7 mm below calyx base, fruits 8--12.5 x (1.7--)2--2.8 cm 40

39. Pedicels articulated 1--2 mm below calyx base or apparently not articulated, fruits up to 9.2 x 2.2 cm (usually much smaller), inflorescence eglandular.....42

40. Standard petal blade speckled orange, dorsal surfaces of all petals densely red glandular, apex of standard claw with a pubescent folded appendage, Belize, Mexico (Yucatan Peninsula) and Guatemala (Peten) .... 13a. **C. yucatanensis** subsp.**yucatanensis**

40. Standard petal blade not speckled orange, dorsal surface of petals with yellow or greenish glands, apex of standard claw with unfolded pubescent ridge or flange ...41

41. Flowers as wide as long, Mexico (eastern Chiapas) and Guatemala..... ..... 13b. **C. yucatanensis** subsp.**chiapensis**

41. Flowers longer than wide, Honduras..... 13c. **C. yucatanensis** subsp.**hondurensis**

42. Secondary venation obscure or lacking on most leaflets, fruit drying purplish and usually densely glandular (at least near base), inflorescence densely white pubescent (as seen under a 10 x lens, the calyx often appears dark purplish black to the naked eye), the hairs sometimes short 43

42. Secondary venation of most leaflets prominent, brochidodromous, fruit drying straw-coloured (not purplish), inflorescence glabrous or pubescent but never densely white pubescent 44

43. Standard petal with orange or reddish markings,flowers in 1--15-flowered racemes (these often aggregated into leafy brachyblasts or congested panicles), leaflets up to 13 x 7.5 mm, Mexico (Sonora and Sinaloa) .....9. **C. palmeri**

43. Standard petal without orange or reddish markings, racemes more than 15-flowered, on woody brachyblasts, leaflets usually over 10 x 7 mm, Mexico (Guerrero)..... ..... 18. **C. epifanioi**

44. Fruit valves densely glandular.....7. **C. acapulcensis**

44. Fruit valves eglandular or at most with a few glands at base near remnants of calyx.. 45

45. Leaflets 14--25 mm wide, bracts 4.5--7 mm long, pedicels 6--10 mm long, pinnae in 2--3 pairs per leaf (plus a terminal pinna) .....7. **C. acapulcensis**

45. Leaflets 2.5--13 mm wide, bracts c. 1.5--4 mm long, pedicels (7--)9--16 mm long, pinnae in 3--6 pairs per leaf (plus a terminal pinna) 46
46. Petiole of pinna longer than rhachis, the leaflets thus clustered at distal end of pinna axis, Mexico (Guerrero-Oaxaca border along Pacific coast)..... 5. **C. nelsonii**
46. Petiole of pinna shorter than rhachis, leaflets not clustered distally, Mexico (Sinaloa, Nayarit and Jalisco) ..... 6. **C. standleyi**
47. Petals various shades of pink or red 48
47. Petals yellow, the standard sometimes with red or orange markings 50
48. Standard petal c 10 x 12 mm, upper lateral petals c 13 x 16 mm, stamens well exserted from corolla, 35 mm long, fruits 9--12 x 2--2.2 cm, Mexico (Oaxaca)..... ..... 12. **C. coccinea**
48. Standard petal up to 10 x 5.5 mm, upper lateral petals up to 10 x 6 mm, stamens slightly exceeding petals in length, fruits up to 6 x 1.7 cm 49
49. Inflorescence rhachis and pedicels densely stipitate-glandular, racemes on short woody brachyblasts, standard petal blade broadly triangular-hastate, pinnae in 1--2 pairs per leaf (plus a terminal pinna), leaflets in 3--4 pairs per pinna, stamen filaments 13--15 mm long, Mexico (Puebla and Oaxaca)..... 19. **C. melanadenia**
49. Inflorescence rhachis eglandular (pedicels occasionally densely stipitate-glandular), racemes erect or pendent, not on short brachyblasts, standard petal blade ovate, pinnae in 3--6 pairs per leaf (plus a terminal pinna), leaflets in (3--)4--6(--10) pairs per pinna, stamen filaments 6.5--11 mm long, Mexico (Puebla, Michoacan and Guerrero) ..... 16. **C. hintonii**
50. Stamens c. twice the length of the petals ..... 15. **C. laxa**
50. Stamens equalling or a little longer than petals 51
51. Flowers laterally compressed, standard with a central red blotch, Mexico (Veracruz and Tamaulipas) ..... 10b. **C. exostemma** subsp.**tampicoana**
51. Flowers not laterally compressed, standard lacking central red blotch 52
52. Leaflet margin and blade glandular, margin crenulate, standard petal panduriform, endemic to southern Baja California..... 41. **C. placida**
52. Leaflet margin glandular, entire or slightly crenulate, blade eglandular, standard petal ovate or orbicular 53

53. Leaflets in (4--)6--11 pairs per pinna, pinnae in (2--)4--6(--7) pairs per leaf (plus a terminal pinna), inflorescence rhachis glabrous, pedicels articulated on the basal ¼..... ..... 17. **C. macvaughii**

53. Leaflets in 2--4 pairs per pinna, pinnae in 1--4 pairs per leaf (plus a terminal pinna), inflorescence rhachis densely white pubescent, pedicels articulated 1--2 mm below calyx or apparently not articulated.....54

54. Standard petal with orange markings, flowers in 1--15-flowered racemes, leaflets up to 13 x 7.5 mm, Mexico (Sonora and Sinaloa) .....9. **C. palmeri**

54. Standard petal without orange markings, racemes more than 15-flowered on woody brachyblasts, leaflets usually over 10 x 7 mm, Mexico (Guerrero) .....18. **C. epifanioi**

55. Stamens red, 2 to 3 times as long as the corolla, 7--9(--12) cm long, pinnae 8--15 pairs per leaf (plus a terminal pinna), leaflets up to 11 x 3 mm, glabrous, usually with a row of submarginal punctate glands, inflorescence a terminal, densely glandular raceme ..... 36. **C. gilliesii**

55. Stamens equalling or slightly longer or shorter than the petals.....56

56. Stems angular,pinnae in 1--2 pairs per leaf (plus a terminal pinna), inflorescence densely glandular, endemic to Chile..... .....46. **C. angulata**

56. Stems terete 57

57. Leaves reduced to one pair of opposite pinnae plus a terminal pinna, ovary with stipitate club-shaped glands especially on the suture, most leaflets of each pinna eglandular, endemic to Peru.....40. **C. ancashiana**

57. Leaves with 2--11 pairs of pinnae plus a terminal pinna (or this occasionally lacking) 58

58. Pinnae with 2--4 pairs of eglandular, glabrous leaflets..... ...44. **C. coluteifolia**

58. Pinnae with (4--)5--13 pairs of leaflets 59

59. Immature fruit with a dense covering of plumose trichomes, terminal leaflets of each pinna 2.5--7 x 1.25--3.5 mm, petals up to 11 mm long, leaflets glabrous to puberulous..... 39. **C. trichocarpa**

59. Immature fruit with simple hairs or glabrous, sessile or short-stalked glands intermixed or these lacking 60

60. Terminal leaflets of each pinna 1.5--4.5 x 0.75--2 mm, petals up to 11.5 mm long, fruit 3--5 x 0.7--1.2 cm 61
60. Terminal leaflets of each pinna 5--20 x 3--7.5 mm, petals 11--20 mm long, fruit 4--10.5 x 1.2--2.2 cm 62
61. Leaflets ovate to cordate, eglandular, the margin entire, the lamina about as long as the distance between each leaflet pair..... ..... 42. **C. exilifolia**
61. Leaflets oblong-obovate to oblong- elliptic, at least the proximal ones on each pinna with glands in deep sulcate depressions, the lamina longer than the distance between each leaflet pair..... 38. **C. mimosifolia**
62. Leaflets pubescent on both surfaces (more densely so on lower surface), a ring of submarginal punctate glands present on the lower surface of leaflet blade .... 43. **C. argentina**
62. Leaflets glabrous on both surfaces (rarely a few small hairs at base on margin), dark punctate glands sparse to dense along margin..... 63
63. Corolla red, pedicels 8--9(--12) mm long, articulated 1--3 mm below calyx, fruit 6.5--9 x 1.6--2.2 cm..... 45. **C. coulterioides**
63. Corolla yellow, pedicels 3--6.5 mm long..... 64
64. Pedicels articulated c 1--1.5 mm below calyx, leaflets in 6--9(--10) pairs per pinna, fruit 4--5.7 x 1.2--1.7 cm, Bolivia and Argentina ..... 37. **C. fimbriata**
64. Pedicels not articulated, leaflets in 10--12 pairs per pinna, fruit 8.5--10.5 x 1.7--2.2 cm, Brazil ..... 35. **C. calycina**

1. **Caesalpinia mexicana** *A. Gray* in Proc. Amer. Acad. 5: 157 (1861). Type: Mexico, Nuevo Leon, near Monterrey, 11 Feb. 1847, *Gregg* s.n. (lectotype GH!, fide McVaugh, 1987).
   Poinciana mexicana (A. Gray) Rose in Contribs. U.S. Nat. Herb. 13: 303 (1911).
   Poincianella mexicana (A. Gray) Britton & Rose in N. Amer. Fl. 23(5): 330 (1930).

Unarmed shrub to small tree, 1--6 m tall, trunk up to c 10 cm in diam.; bark greenish-grey, smooth with raised orange-brown or pale grey lenticels in semaphore lines, inner bark green; whole plant glabrous or with various degrees of pubescence. *Leaves* bipinnate; stipules ovate, c 5 mm long, apex acute to rounded, base cordate-auriculate below point of attachment, margin ciliate and glandular, early caducous; petiole 2--8 cm long, glabrous to pubescent, eglandular; rhachis 4--12 cm long, glabrous to pubescent, eglandular; pinnae in 2--4(--5) opposite pairs plus a terminal pinna; leaflets in (2--)3--5(--6) opposite pairs, petiolulate, terminal leaflets obovate-elliptic to oblong-elliptic, 1.1--3.5 x 0.7--1.8 cm, median leaflets obovate-elliptic to ovate or suborbicular, 1--2.8 x 0.7--1.8 cm, apices of all leaflets obtuse, rounded, truncate or shallowly emarginate, bases inequilateral, margins ± revolute, both surfaces of blade glabrous to moderately pubescent, or with just a small tuft of hairs in main vein axis on lower surface; main vein prominent below, secondary veins brochidodromous; glands on leaflet blades lacking but gland-tipped cone-shaped appendages clustered into a corona at pinnae insertions and a single gland-tipped appendage below each leaflet pulvinule, these very evident on very juvenile foliage (see *Hughes* 1604) but apparently lacking on some mature foliage. *Inflorescence* a compact or long, lax, many-flowered axillary or terminal erect raceme, 4--30 cm long, rhachis, pedicels and calyces moderately pubescent or glabrous; bracts ovate, concave, 0.5--2 mm long, margin ciliate, early caducous; pedicels 1.3--3 cm long,if pubescent the hairs densest at point of articulation, 2--7 mm below calyx. *Calyx* base tapering into upper section of pedicel, lobes 6--9 mm long, densely pubescent on inner surface, lower lobe cucullate in bud, imbricate at anthesis. *Corolla* bright yellow; standard petal spotted or faintly streaked orange-red at base, blade obovate to cordate, apex emarginate, 10--12 x 8--10 mm (including a 1--1.5 mm claw), dorsal surface stipitate-glandular with yellow or orangish glands on the basal ½, blade base and claw pubescent, claw margin stipitate-glandular, inner surface of claw lacking an appendage or

thickened ridge; upper lateral petals obovate-suborbicular to cordate, apex emarginate, 12--14 x 9--10 mm (including a 1.5--2 mm claw), base of blade and claw glandular on dorsal surface, claw sparsely pubescent on inner surface; lower laterals obovate-elliptic to cordate, apex emarginate, 13--14 x 10--10.5 mm (including a 2 mm claw), claw glabrous, glandular. Stamen filaments 12--13 mm long, pubescent on basal ½--¾, anthers 2 x 0.75 mm. Ovary pubescent and eglandular or densely glandular, 3--5(--6)-ovulate; style curved, c 10 mm long; stigma a terminal, fringed, tubular or funnel-shaped chamber. *Fruit* a subligneous, elastically dehiscent pod, 4.4--7.5 x 1.4--2 cm (including a 1.5 mm beak), glabrous to moderately pubescent (most evident on the suture), eglandular or sparsely glandular with sessile or short-stalked glands, (1--)2--5-seeded. *Seeds* orbicular or cordate, 9--10 x 7.5--8.5 x 1.5--2.5 mm, dark brown or olive green-brown, shiny. *Seedling* germination phaneroepigeal, cotyledons foliaceous, apex rounded, base cordate, tardily caducous, first eophyll pinnate with 3--4 opposite pairs of leaflets, second eophyll alternate to first, pinnate with 3--4 pairs of leaflets or bipinnate with one opposite pair of pinnae plus a terminal pinna, each with 2 pairs of opposite leaflets, hypocotyl glabrous, epicotyl glabrous, sparsely glandular with a few short stipitate glands. (Figs. **14** & 21F, Map 3).

DISTRIBUTION. Southern Texas; central and eastern Mexico: Nuevo Leon, San Luis Potosi, Tamaulipas, Queretaro, Hidalgo and Veracruz. Known to have been cultivated as an ornamental shrub in Cuba, Hawaii, Iraq, Senegal and the U.S.A.

MEXICO: Nuevo Leon, Monterrey, June 1911, *Arsène* 6197 (US!); Rancho El Pinto, Mpio. de Hualahuises, 12 Aug. 1986, *Castillión* 629 (K!, MEXU!); Mpio. Linares, bridge E of Los Pinos, 5 July 1985, *Cowan et al.* 5445 (TEX!); c 36 miles SE of Montemorelos, 17 July 1971, *Dwyer et al.* 18 (MEXU!, NY!); Monterrey, 1848, *Eaton & Edwards* 14 (K!); *Eaton & Edwards* ? 80 (K!); 1846, *Edwards & Eaton* s.n. (NY!); 7 miles SE of Santa Catarina bridge, Monterrey, 11 Nov. 1959, *Graham & Johnston* 4621 (MEXU!); nr. Monterrey, 11 Feb. 1847, *Gregg* s.n. (GH!); Mpio. Linares, nr. bridge over Rio Pabillo, 28 Oct. 1982, *Grimes et al.* 2362 (NY!, TEX!); below Ebanito, 12 March 1980, *Hinton et al.* 17744 (MEXU!, TEX!); 26 Sept. 1979, *Hinton et al.* 17624 (MEXU!); 16 km S of Linares, 26 April 1985, *Hughes* 691 (K!, MEXU!); Monterrey, Silla Mt., 2 Oct. 1937, *Kenoyer* 238 (F!); Mpio. Villa de Santiago, 3 July 1941, *Leavenworth & Leavenworth* 813 (F!); 10 miles W of Monterrey, 8 July 1953, *Manning & Manning* 53100 (MEXU!); Rio Ramos, 2 Nov. 1970, *Marroquín* 2022 (F!); Monterrey, Sierra de Chipinque, 6 March 1981, *Mendoza* 146 (MEXU!); nr. Monterrey, July 1933, *Mueller & Mueller* 514 (F!, TEX!); Sierra Madre,

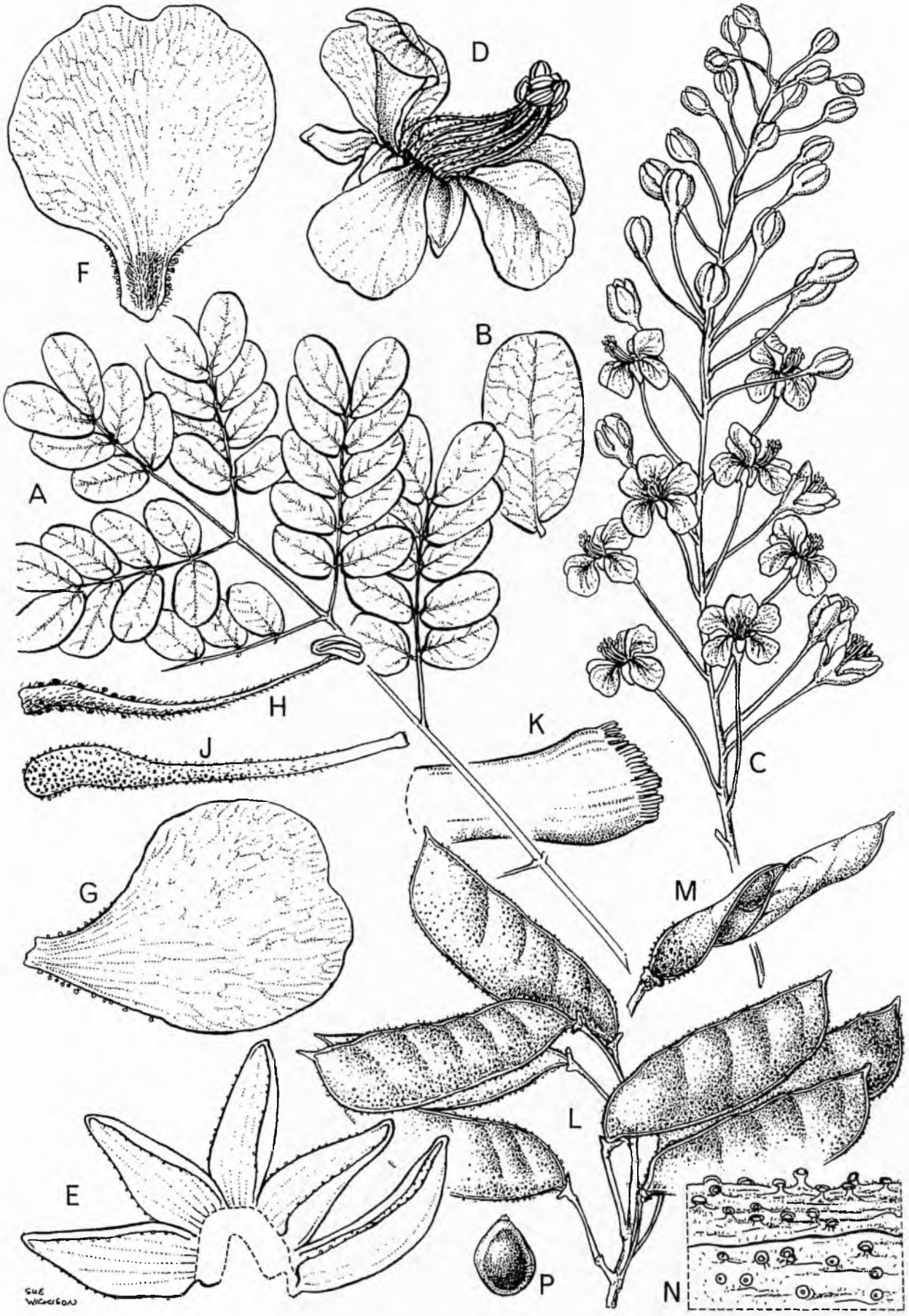
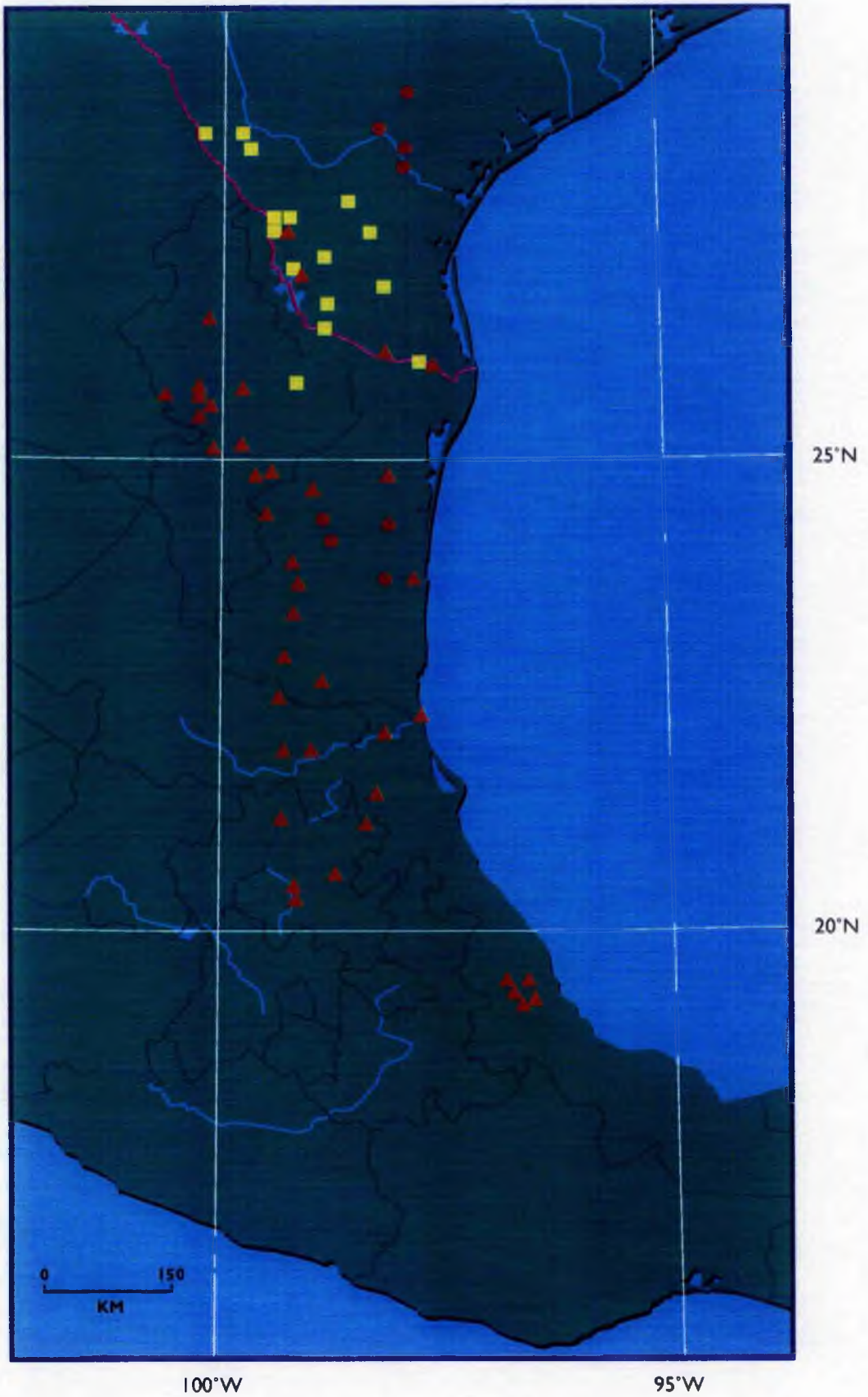


FIG. 14. *Caesalpinia mexicana*. **A** part bipinnate leaf x 1; **B** leaflet undersurface x 3; **C** inflorescence x 1; **D** flower x 3; **E** calyx opened out x 4½; **F** standard petal x 6; **G** lateral petal x 6; **H** stamen x 6; **J** gynoecium x 6; **K** stigma x 40; **L** fruits x 1; **M** twisted valve of fruit x 1; **N** glands on fruit x 24; **P** seed x 1½. **A–L** from *Pringle* 1908, **M–P** from *Berlandier* 2371 [= 941]. Drawn by Sue Wickison.

Distribution of *Caesalpinia caudata* (■) *C. mexicana* (▲) and *C. phyllanthoides* (●) in south eastern U.S.A. and eastern Mexico



Monterrey, 1934, *Mueller & Mueller* 3559 (MEXU!); Monterrey, 1880, *Palmer* 282 (K!); nr. Monterrey, 2 (fl.) & 22 (fr.) July 1888, *Pringle* 1908 (BR!, E!, F!, K!, M!, MEXU!); nr. Monterrey, 4 Sept. 1902, *Pringle* 9724 (F!, K!, MEXU!); Monterrey, 30 March 1946, *Royal* s.n. (MEXU!); 7 km W of Rayones on road to Montemorelos, 24 May 1982, *Silva* 106 (MEXU!); 30 miles S of Monterrey at Cola de Caballo Falls, 18 May 1987, *Simpson* 18-3-87-3 (TEX!); 40 miles S of Monterrey, 3 April 1947, *Smith & Barkley* 17M170 (F!, TEX!); 4 km N of Hualahuises, 6 Aug. 1982, *Torres et al.* 963 (MEXU!); 14 km S of Sabinas Hidalgo, 14 July 1979, *Trott et al.* 108 (MEXU!); SW of Monterrey, 8 June 1962, *Webster et al.* 11222 (MEXU!); nr. Montemorelos, 14 Oct. 1980, *Wussow & Landry* 287 (LSU!); **San Luis Potosi**, 5 km W of San Antonio, 9 Oct. 1978, *Alcorn* 1942 (NY!, TEX!); Taujasnec, Mpio. San Antonio, 28 Feb. 1979, *Alcorn* 2470 (MEXU!, TEX!); 5 km W of Nuevo Morelos, 2 March 1949, *Clausen* 7426 (MEXU!, NY!); c 20 km W of Ciudad Valles, 11 Feb. 1992, *Hughes et al.* 1604 (K!); c 3 km S of Ciudad Valles, 12 Feb. 1992, *Hughes et al.* 1606 (K!); San Luis Potosi to Tampico, Dec. 1878-Feb. 1879, *Palmer* 1054 (K!); Las Palmas, 4 March 1899, *Pringle* 6986 (BR!, E!, F!, K!, M!, MEXU!, MO!); N outskirts of Valles, 5 April 1955, *Wiggins* 13348 (US!); **Tamaulipas**, Sierra de San Carlos, vicinity of San José, 7 July 1930, *Bartlett* 10141 (F!, LL!, MEXU!); 8 km N of Río Corona, 27 km N of Ciudad Victoria, 9 April 1949, *Clausen* 7536 (MEXU!); 4 miles E of Ocampo, 5 March 1960, *Crutchfield & Johnston* 5191 (MEXU!); 12 miles S of Ciudad Mante, 1 April 1975, *Harriman* 10748 (F!); 30 km SW of Ciudad Victoria, nr. Altas Cumbres, 4 Nov. 1987, *Hughes* 1054 (K!); c 4--5 miles S of Ciudad Mante,18 Feb. 1961, *King* 3835 (NY!, TEX!, US!); c 13 miles SW of Ciudad Victoria, 9 Nov. 1975, *Lasseigne* 4879 (MEXU!, MO!, NY!); c 31 miles SE of Ciudad Victoria on highway 85 to Ciudad Mante, 8 Nov. 1975, *Lasseigne* 4874 (MEXU!); marker 184 on Mexico 180, 7 April 1987, *Lievens & Gregory* 2218 (LSU!); W from Ciudad Victoria to Jaumave, 21 July 1953, *Manning & Manning* 53405 (MEXU!); 6.2 miles S of San Fernando, 9 June 1966, *Mathwig & Janzen* 1077 (MEXU!); 4 miles E of highway 101, La Pesca road, 23 June 1965, *Maxwell* 17 (NY!); 3 km SE of Rancho Las Urracas, E of San Fernando,25 Jan. 1964, *Medrano* 726 (MEXU!, US!), 10 km SW of La Oveja, 23 May 1970, *Medrano et al.* 2907 (MEXU!); 30 km W of turnoff to Mendez Viniendo de Reynosa, 9 Feb. 1969, *Medrano et al.* 2015 (MEXU!); 12.5 km SE of Río San Marcos bridge on outskirts of Ciudad Victoria, 7 March 1983, *Nee & Taylor* 25789 (F!, MEXU!); SE outskirts of Ciudad Victoria, 22 Oct. 1981, *Nee* 22215 (MEXU!); nr. Tampico, 3--6 June 1910, *Palmer* 571 (F!, K!); nr. Tampico, Jan. 1910, *Palmer* 177 (F!, K!); nr. Victoria, 1 Feb. -- 9 April 1907, *Palmer* 26 (F!, K!); nr. Victoria, Feb--April 1907, *Palmer* 224 (F!,K!); Sierra of Victoria, Jaumave, Feb. 1933, *Rozynski* 735 (F!); Jaumave, March 1932, *Rozynski* 357 (F!, NY!); nr. Ciudad Victoria, road to Jaumave, 31 Aug. 1950, *Sharp et al.* 50356 (NY!); 19 miles S of Ciudad Victoria on highway 85, 19 March 1987, *Simpson* 19-3-87-2 (TEX!); Mpio. San Carlos, between El Lantrisco and Santa Teresa, 10 March 1970, *Toledo & Medrano* 2813 (MEXU!); **Queretaro**, La Vuelta,18 km NE of Landa de Matamoros, 28 April 1982, *Hernández & Tenorio* 719 (MEXU!); **Hidalgo**, c 3 km WNW of Huejutla de Reyes, 12 Feb. 1992, *Hughes et al.* 1609 (K!); 42 km E of Ixmiquilpan, 2 May 1976, *Medrano et al.* 8892 (MEXU!); Gilotla, Mpio. of Eloxochitlan, 9 May 1981, *Magaña et al.* 6081 (MEXU!); Mpio. Cardonal, nr. San Cristóbal, 21 March 1977, *Rzedowski* 34682 (MEXU!, NY!); **Veracruz**, Mpio. Tempoal, road Horcones to Chicayan, 25 Aug. 1979, *Calzada* 5559 (F!); Mpio. Emiliano Zapata,

road Jalapa to Veracruz, 14 Feb. 1976, *Calzada* 2199 (F!); Mpio. Naolinco, La Bajada, Almo longa, 15 March 1978, *Calzada* 4270 (MEXU!, TEX!); road Revendadero to Temapache, 7 Sept. 1980, *Calzada et al.* 6247 (F!); 2 km from Jalcomulco to Tuzamapan, Mpio. Coatepec, 28 July 1979, *Castillo & Tapia* 787 (MBM!, MEXU!); Barra Platanar, 15 July 1972, *Dorantes et al.* 1345 (BR!); Mpio. of Dos Rios, Cerro Gordo, 25 March 1975, *Ventura* 11131 (MEXU!); Mpio. of Jalapa, Seis de Enero, 14 April 1975, *Ventura* 11192 (MEXU!); **U.S.A., Texas**, Webb Co., Laredo, 18 April 1963, *Balleza & Valdez* 230 (TEX!); Hidalgo Co., route 83 between McAllen and Pharr, 8 Feb. 1969, *Correll* 36754 (K!, LL!, TEX!); Sullivan City, 8 Feb. 1969, *Correll* 36753 (K!, TEX!); Webb Co., Laredo, 27 March 1965, *Guajardo* 1 (TEX!); Zapata Co.,10 miles N of Zapata, 3 Nov. 1940, *Hamby* 1712 (TEX!); Hidalgo Co., 3 miles N of Edenburgh,29 Feb. 1944, *Painter & Barkley* 14449 (K!, LL!, TEX!); Webb Co., Laredo, 6 April 1965, *Webber* 6 (LL!).

NEOTROPICAL CULTIVATED SPECIMENS: Cuba, Las Villas, nr. Cienfuegos, grounds of Harvard Botanical Garden, 24 Feb. 1956, *Morton* 10603 (US!); **U.S.A., Texas**, San Patricio Co., S of Odum, 12 Oct. 1974, *Bauml et al.* 74-346 (TEX!); Webb Co., Laredo, 14 March 1964, *Guardado* 50 (TEX!); Brooks Co., 20 Jan. 1981, *Nee* 20091 (F!); Brownsville, 1 July 1936, *Runyon* 5464 (TEX!); 20 Oct. 1923, *Runyon* 565 (TEX!); 1 May 1924, *Runyon* 5441 (TEX!); 1 Feb. 1925, *Runyon* 5443 (TEX!); 1 Aug. 1936, *Runyon* 3550 (TEX!); 14--15 March 1923, *Tharp* 1837 (TEX!); Duval Co., San Diego, 24 March 1956, *Thompson & Turner* 38 (TEX!); Brownsville, 20 March 1907, *York* 133 (TEX!); **Florida**, Dade Co. Miami, Fairchild Tropical Garden, 21 May 1988, *Ramirez-Domenech & Lievens* 2036 (LSU!).

ECOLOGY. Low deciduous forest, open semi-arid scrub, 'matorral alto subinerme', on sandy loam and limestone, open rocky ledges,15--1100 m.

PHENOLOGY. Flowering from January to November, fruiting from February to November.

VERNACULAR NAMES. "Tsibiliim" (Huastec name, Mexico: San Luis Potosi), "Potro", "Hierba del Potro" (Mexico: Tamaulipas).

NOTES. *C. mexicana* and species closely related to it, namely *C. standleyi, C. phyllanthoides, C. nelsonii* and *C. pannosa*, all require further study. New morphological data may result in some taxonomic replacements and consequent nomenclatural alteration. *Berlandier* 2371 (= 941), a paratype of *C. mexicana*, comes from San Carlos but on the Kew specimen no further locality detail is given. It seems probable that, of the several San Carlos locations in Mexico, Berlandier's specimen was collected in Coahuila, near the Texan border. If that assumption is correct then Gray's citation, in the protologue of *C. mexicana*, of the species in Chihuahua would seem to be erroneous.

2. **Caesalpinia phyllanthoides** *Standley* in Contribs. U.S. Nat. Herb. 23: 425 (1922). Type: Mexico, Tamaulipas, Hacienda Buena Vista, 18 June 1919, *Wooton* s.n. (holotype US!, isotype NY!).
   Poincianella phyllanthoides (Standley) Britton & Rose in N. Amer. Fl. 23(5): 332 (1930).

Unarmed, rhizomatous colonial woody-based herb to shrublet, c 30--80 cm tall, stems with dense, white, pustular lenticels, puberulous, glabrescent, sparsely glandular or eglandular. *Leaves* bipinnate; petiole 1.3--4.1 cm long, glabrous or puberulous and with a few stipitate-glands near base; rhachis 2.5--5 cm long, glabrous, sometimes with a few short-stalked glands; pinnae in 3--4 opposite pairs plus a terminal pinna, gland-tipped appendages clustered at pinnae insertions; leaflets in 2--3 opposite pairs, petiolulate, a minute gland-tipped appendage at base of each petiolule on lower side, blade obovate to elliptic-orbicular, apex rounded to obtuse, margin thickened and often drying purplish, terminal leaflets 4.5--11 x 3--7 mm, medians 4--11 x 3--9 mm, both surfaces glabrous; blade ± fleshy, venation obscure, main vein ± evident on lower surface, secondary veins brochidodromous, eglandular. *Inflorescence* a terminal or lateral 15--20-flowered raceme; bracts ovate, acute, c 2.5--4.5 mm long, puberulous, margin fimbriate-glandular; pedicel 7--14 mm long, puberulous, stipitate-glandular near apex, articulated c 1 mm below calyx but zone of articulation not clear. *Calyx* puberulous and stipitate-glandular, lower lobe 5--7.5 mm long, other four 4.5--6 mm long, margins fimbriate-glandular. *Corolla* yellow; standard petal blade ovate-elliptic, 11 x 7--9 mm (including a 0.5 mm claw), claw margin pubescent, a small triangle of hairs at claw apex on inner surface (the petal lacking a ridge or flap of thickened tissue at claw apex), a few glands on blade margin near base; upper lateral petals obovate, 11 x 6 mm (including a 1 mm claw), claw sparsely hairy and short-stalked glandular; lower lateral petals oblanceolate, 12 x 4.5 mm (including a 2 mm claw), claw stipitate-glandular, glabrous. Stamen filaments 9--10 mm long, pubescent on basal ½; anthers 1.5 x 0.75 mm. Ovary puberulous, especially on the suture, densely short-stalked glandular over whole surface; style 10.5 mm long, glabrous, bent upwards from apex of ovary; stigma a terminal, flared or funnel-shaped, fringed chamber. *Fruit* not seen in this study but described by Standley (1922) and Britton & Rose (1930) as elastically

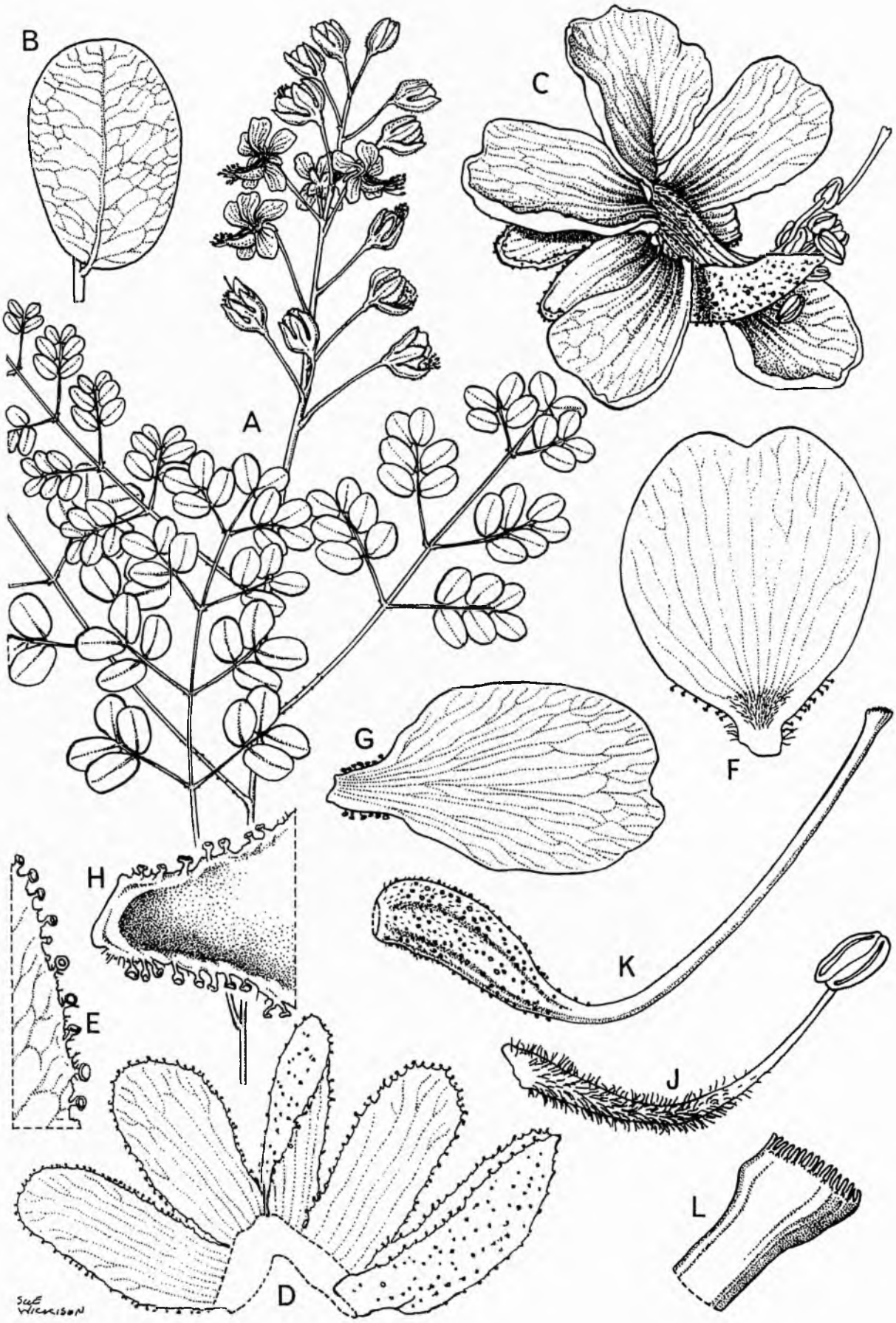


FIG. 15. *Caesalpinia phyllanthoides*. **A** inflorescence and foliage x 1; **B** leaflet undersurface x 6; **C** flower x 4½; **D** calyx opened out x 6; **E** calyx lobe margin detail x 40; **F** standard petal x 6; **G** upper lateral petal outer surface x 6; **H** detail of lateral petal claw x 18; **J** stamen x 9; **K** gynoecium x 9; **L** stigma x 40. **F** from *Nee* 32666, the rest from *Bartlett* 10616. Drawn by Sue Wickison.

dehiscent, 2.5 x 1.3 cm, glabrous but with a few scattered dark glands, 1--2-seeded. (Fig. 15, Map 3).

DISTRIBUTION. U.S.A. in SE Texas, and Mexico in the state of Tamaulipas.

U.S.A.: Texas, Jim Wells Co., c 6 mi. N of Orange Grove, 15 March 1955, *Jones* 1087 (TEX!); Jim Wells Co., W side of FM 534, 0.6--0.7 mi. S of rd. to Pernitas, 21 March 1988, *Orzell & Bridges* 6002 (TEX!); Live Oak Co., Three Rivers, 3 May 1939, *Parks & Cory* 31410 (TEX!); Live Oak Co., cult. at Apicultural Lab. San Antonio, originally from Dinero, 1 May 1945, *Parks* s.n. (TEX!); MEXICO, Tamaulipas, Cerro de la Tamaulipeca, nr. San Miguel, 26 July 1930, *Bartlett* 10616 (F!); 6 mi. E of Panales, 26 April 1960, *Crutchfield & Johnston* 5343 (MEXU!, TEX!); 5 mi. W of Loreto, 8 Feb. 1960, *Crutchfield & Johnston* 5071 (MEXU!, TEX!); 5 mi. E of San Carlos on rd. to Padilla, 13 Dec. 1959, *Crutchfield & Johnston* 4997A (TEX!); 11 mi. N of Soto la Marina on rd. to Jimenez, 12 Dec. 1959, *Crutchfield & Johnston* 4978B (TEX!); Morales, 15 Feb. 1939, *Le Sueur* 191 (F!); San José, 17 Feb. 1939, *Le Sueur* 192 (TEX!); Mpio. Santander Jimenez, 26 km NE of Nueva Ciudad Padilla, 16 Aug. 1986, *Nee* 32666 (K!, NY!); Hacienda Buena Vista, 18 June 1919, *Wooton* s.n. (holotype US!, isotype NY!).

ECOLOGY. Subtropical arid thorn scrub on limestone outcrops or sandy loam soils, c 30--600 m.

PHENOLOGY. Flowering February to August, information on fruiting not available for this study.

NOTES. A little-known species closely related to *C. mexicana* but seemingly distinct by its rhizomatous, colony forming habit and regularly orbicular-elliptic leaflets.

3. **Poincianella robinsoniana** *Britton & Rose* in N. Amer. Fl. 23(5): 330 (1930). Type: Mexico, Jalisco, Zapotlán, 25 May 1893, *Pringle* 5467 (holotype GH!, isotype MEXU!).

   Caesalpinia mexicana A. Gray var. *pubescens* B.L. Rob. & Greenm. in Amer. Acad. Proc. 29: 386 (1894). Type as above.

Unarmed shrublet. *Leaves* bipinnate; petiole 1.7--3.5 cm long, pubescent; rhachis c 2.4 cm long or lacking; pinnae in 1--2 opposite pairs plus a terminal pinna; leaflets in 2--3 opposite pairs, elliptic-obovate, 15--17 x 8--10 mm, glabrous to pubescent on both

surfaces; main vein prominent below, secondaries brochidodromous; eglandular. *Inflorescence* an axillary or terminal, glabrous, c 30-flowered raceme; pedicels 10--11 mm long, glabrous, articulated 2 mm below calyx. *Calyx* upper and lateral lobes 5--6 mm long, lower lobe 7 mm long. Standard petal blade cordate-orbicular, 6 x 4--5 mm (including a 2 mm claw), dorsal surface and apex of claw stipitate-glandular, claw densely pubescent on margins and inner surface, stipitate-glandular on margins; upper lateral petals depressed orbicular, 8 x 6 mm (including a 1.5 mm claw), claw margins stipitate-glandular, a small tuft of hairs on inner surface in middle; lower lateral petals obovate-oblanceolate, 10 x 4 mm (including a 1.5 mm claw), claw almost glabrous, margins stipitate-glandular; all five petals with glandular margins. Stamen filaments 10--11 mm long, densely pubescent on basal ¾ or for entire length. Ovary densely tomentose, 2--3-ovulate; style c 8 mm long; stigma a terminal, fringed chamber. *Pod* subligneous, elastically dehiscent, c 4.5 x 1.8 cm, very finely puberulous, the hairs most evident on the margins, 2--3-seeded. (Map 6).

DISTRIBUTION. Only known from the type locality in Jalisco, Mexico.

MEXICO: Jalisco, near Zapotlán, 25 May 1893, *Pringle* 5467 (holotype GH!, isotype MEXU!).

ECOLOGY. 'Dry hills'.

PHENOLOGY. The type material, in flower and fruit, was collected in May.

NOTES. The holotype specimen of *Pringle* 5467 at GH appears to be a mixed collection. The fruiting branchlet (top right of sheet), together with fruit valves in a packet (top left) are not the same as the fruiting specimen (on the left side of the sheet). The fruiting branchlet (top right) appears to be closer to *Caesalpinia standleyi* (Britton & Rose) Standley. *Poincianella robinsoniana* (no combination has ever been made in *Caesalpinia*) is, however, probably just a form of *C. standleyi* and the herbarium specimen in question possibly represents part of the range of population variation in *C. standleyi* sens. lat. Alternatively, *P. robinsoniana* is perhaps just a western form of *C. mexicana* A. Gray, as indicated by its original description as *C. mexicana* var. *pubescens* B.L. Rob. & Greenm. *C. standleyi*, in western Mexico, and *C. mexicana*, essentially in eastern Mexico, both have pubescent and glabrous forms; *C. mexicana* intergrades through *C. standleyi* to *C. caladenia* in Sonora and *C. acapulcensis* in Colima, Michoacan and

Guerrero. McVaugh (1987) placed *P. robinsoniana* in synonymy under *C. mexicana* which was a pragmatic decision but I choose to temporarily keep it separate pending the collection of more material from the type locality in an attempt to discover if the one collection by which the species is known is idiosyncratic or if the minor characters by which the specimen can be distinguished are consistent. I feel it unwise to make a new combination in *Caesalpinia* for *P. robinsoniana* as it is most unlikely that it is worthy of recognition at the rank of species. The fruiting branchlet (left of sheet) has bipinnate leaves with all leaflets densely pubescent while other leaves on the same twig have all leaflets glabrous or almost so. The presence or absence of leaflet indumentum is a feature of *Caesalpinia* morphology that has been erroneously used to separate various species and infraspecific taxa.

4. **Caesalpinia pannosa** *Brandegee* in Proc. Calif. Acad., Second Series, 2: 150 (1889) and 3: 130 (1891). Type: Baja California, San Gregorio, 1 Feb. 1889, *Brandegee* s.n. (lectotype UC!, chosen here).

   Poinciana pannosa (Brandegee) Rose in Contribs. U.S. Nat. Herb. 13: 303 (1911).

   Poinciana californica (A. Gray) Rose, loc. cit. (1911).

   Caesalpinia mexicana A. Gray var. *californica* A. Gray in Proc. Amer. Acad. 5: 157 (1861). Type: Baja California, Cape St. Lucas, Aug. 1859--Jan. 1860, *Xantus* 29 (lectotype GH!, chosen here, isolectotype NY!).

   Caesalpinia californica (A. Gray) Standley in Contribs. U.S. Nat. Herb. 23: 426 (1922).

   Poincianella pannosa (Brandegee) Britton & Rose in N. Amer. Flora 23(5): 331 (1930).

   Poincianella californica (A. Gray) Britton & Rose, loc. cit. (1930).

   Caesalpinia arenosa Wiggins in Contribs. Dudley Herb. 3(3): 68 (1940). Type: Baja California, 4 miles S of Guadalupe, 21 March 1935, *Whitehead* 839 (holotype DS).

Unarmed single or multiple-stemmed shrub, occasionally ± scandent (e.g. *Gentry* 4365, *Lewis et al.* 2041), sometimes ± prostrate,(0.25--)1--6(--6.5) m tall, main stems 1--

5(--10) cm in diam.; bark variable, grey or greyish-white splitting vertically to reveal a green under bark, the paper-thin outer bark then peeling and rolling back, white lenticels sparse or dense, usually pustular; heart wood dark brown, young stems pinkish-red, ± flexuous, sometimes zig-zag, glabrous or pubescent, glandular or eglandular. *Leaves* bipinnate; stipules orbicular, foliaceous, ciliate, caducous; petiole 1.6--4.2 cm long, glabrous and stipitate-glandular or pubescent; rhachis 2--6 cm long, glabrous and stipitate-glandular or pubescent; pinnae in (1--)2--4 opposite pairs, minute glandular appendages clustered at pinnae insertions; leaflets in 3--5(--6) opposite pairs, ± fleshy, green with a bluish tinge and pinkish-red margins when juvenile, glandular stipel-like appendages below leaflet petiolule, terminal leaflets broadly elliptic to obovate, 8--14 x 4--9 mm, median leaflets broadly elliptic, 6.5--20 x 4--11 mm, leaflet apices truncate, rounded or shallowly emarginate, often mucronate, both surfaces glabrous to densely pubescent; venation obscure except for main vein on lower surface, glands lacking. *Inflorescence* an axillary or terminal, 10--25(--30) cm long, c 30--75-flowered raceme (uncommonly a terminal panicle), rhachis, pedicels and calyces glabrous to densely pubescent, eglandular to densely stipitate-glandular; bracts ovate-lanceolate, acuminate to lanceolate-cuspidate, 4.5--6.5 mm long, the apices reflexed or not, glabrous to pubescent or with only the margins ciliate, eglandular or with the margins fimbriate glandular, rarely a pair of bracteoles on the basal ½ of the pedicel (e.g. *Webster* 19561); pedicels 7--16 mm long, articulated 4--11 mm below calyx (well below to slightly above the middle of the pedicel). *Calyx* lower lobe cucullate, 4.5--7 mm long, other lobes 4--7 mm long, all lobes reddish or pale orangish-brown, where they overlap in bud yellow, glabrous to densely pubescent, margins ciliate or not, glandular or eglandular, inner surface moderately appressed puberulous to densely sericeous, sepals reflex at anthesis and fold back to original position as flower fades. *Corolla* lemon or buttermilk yellow, three upper petals reflex, two lower laterals held downwards; standard petal blade ovate-orbicular to ovate-elliptic, 8--12 x 5.5--6.5 mm (including a 1--2.5 mm claw); upper lateral petals ovate to ovate-elliptic, 8--12.5 x 6--6.5 mm (including a 1--3 mm claw); lower laterals ovate-elliptic, 8--12 x 5--5.5 mm (including a 1--2 mm claw), all petals with outer surface moderately to densely glandular with red stipitate or sessile glands, claws glabrous and eglandular, that of the standard without an appendage. Stamen filaments 10--12 mm long, one on either side of the vexillary stamen with a basal appendage which, together with the slightly sunken vexillary

filament, protect the staminal fenestrae and thus the nectar, filaments white pubescent on basal ½--¾, alternate filaments sparsely stipitate-glandular on upper ¼--½; anthers pale yellow, 1.25 x 0.75 mm. Ovary densely white pubescent or glabrous, glandular near the base or densely glandular over entire surface, young glands green, maturing red, 3--5-ovulate; style c 10 mm long, thickened towards apex; stigma a terminal, tubular, unfringed chamber. *Fruit* an elastically dehiscent, subligneous pod, 4--6 x 1.3--1.75 cm (including a 2--3 mm beak), glabrous to densely pubescent, eglandular to densely glandular with red, sessile or short-stalked glands, 2--5-seeded. *Seeds* ovate, 7.5--8 x 6--7 x 1--1.5 mm, pale brown, orangish-brown or dark brown, shiny. *Seedling* germination phaneroepigeal, cotyledons foliaceous, apex rounded, base cordate, tardily caducous, first eophyll pinnate with 3--4 pairs of opposite leaflets, second eophyll bipinnate with 1 pair of pinna and a terminal pinna, each with 2 pairs of opposite leaflets, hypocotyl glabrous, epicotyl glabrous and glandular. (Figs. 1D, 5P, 11C, **16**, 17, Map 4).

DISTRIBUTION. Endemic to Baja California.

MEXICO: Baja California, 15 km E of Cabo San Lucas, 13 April 1977, *Ahuatzin* s.n. (MEXU!); 6.4 miles S of La Paz, 24 Oct. 1977, *Ames et al.* 77--54 (MEXU!); 3.8 miles N of Loreto, 28 Oct. 1977, *Ames et al.* 77--98 (MEXU!); San José del Cabo, 23 April 1897, *Anthony* 331 (E!, F!, K!); San Gregorio, 1 Feb. 1889, *Brandegee* s.n. (lectotype UC!); Todos Santos, 31 Jan. 1890, *Brandegee* s.n. (NY!); Rio del Salada, 20 Oct. 1977, *Breedlove & Axelrod* 43124 (MEXU!); 23.5 miles SE of El Cien, 18 Oct. 1981, *Burgess et al.* 6184 (MEXU!); 4.7 miles NE of Agua Amarga, 17 Oct. 1981, *Burgess & Newland* 6154 (MEXU!); Sierra de la Giganta, 20 Sept. 1965, *Carter* 4998 (MEXU!, NY!); Rancho Aguajito, NW of Loreto, 26 Sept. 1967,*Carter & Moran* 5251 (NY!, TEX!); *Carter & Moran* 5252 (NY!); 13 km N of San Domingo, 6 Dec. 1947, *Carter et al.* 2133 (K!); 23 km SW of Comondú, 5 Dec. 1947, *Carter et al* 2124 (K!, MEXU!); 3.2 km N of San José del Cabo, 18 Dec. 1947, *Carter et al.* 2285 (K!); Magdalena Plain, 42 miles S of Comondú, 6 Aug. 1955, *Chambers* 810 (MEXU!); 4 miles SE of Triunfo, 18 Feb. 1947, *Constance* 3162 (F!, K!, LL!, MEXU!, NY!); 3 km E of San Jorge, 27 Feb. 1990, *Contreras* 2702 (K!); *Contreras* 2703 (K!); 11 km E of Cabo San Lucas, 27 Feb. 1990, *Contreras* 2704 (K!); 33 km N of Cabo San Lucas, 28 Feb. 1990, *Contreras* 2712 (K!); near Bahia de Todos Santos, 28 Feb. 1990, *Contreras* 2713 (K!); *Contreras* 2715 (K!); 60 km N of La Paz, 1 March 1990, Contreras 2727 (K!); *Contreras* 2726 (K!); 18 km S of La Paz, 26 Feb. 1990, *Contreras* 2696 (K!); 22 km SW of San Pedro, 28 Feb. 1990, *Contreras* 2721 (K!); highway 1, 83.7 miles SE of junction with highway 22 in Constitucion, 9 Jan. 1983, *Daniel* 2439 (NY!); Punta Frailes, 16 Feb. 1940, *Dawson* 1125 (F!); Santiago, 20 March 1939, *Gentry* 4365 (K!); La Burrera, 25 March 1939, *Gentry* 4438 (K!); San Juanico, 6 March 1939, *Gentry* 4298 (K!); 17 km S of La Paz, 15

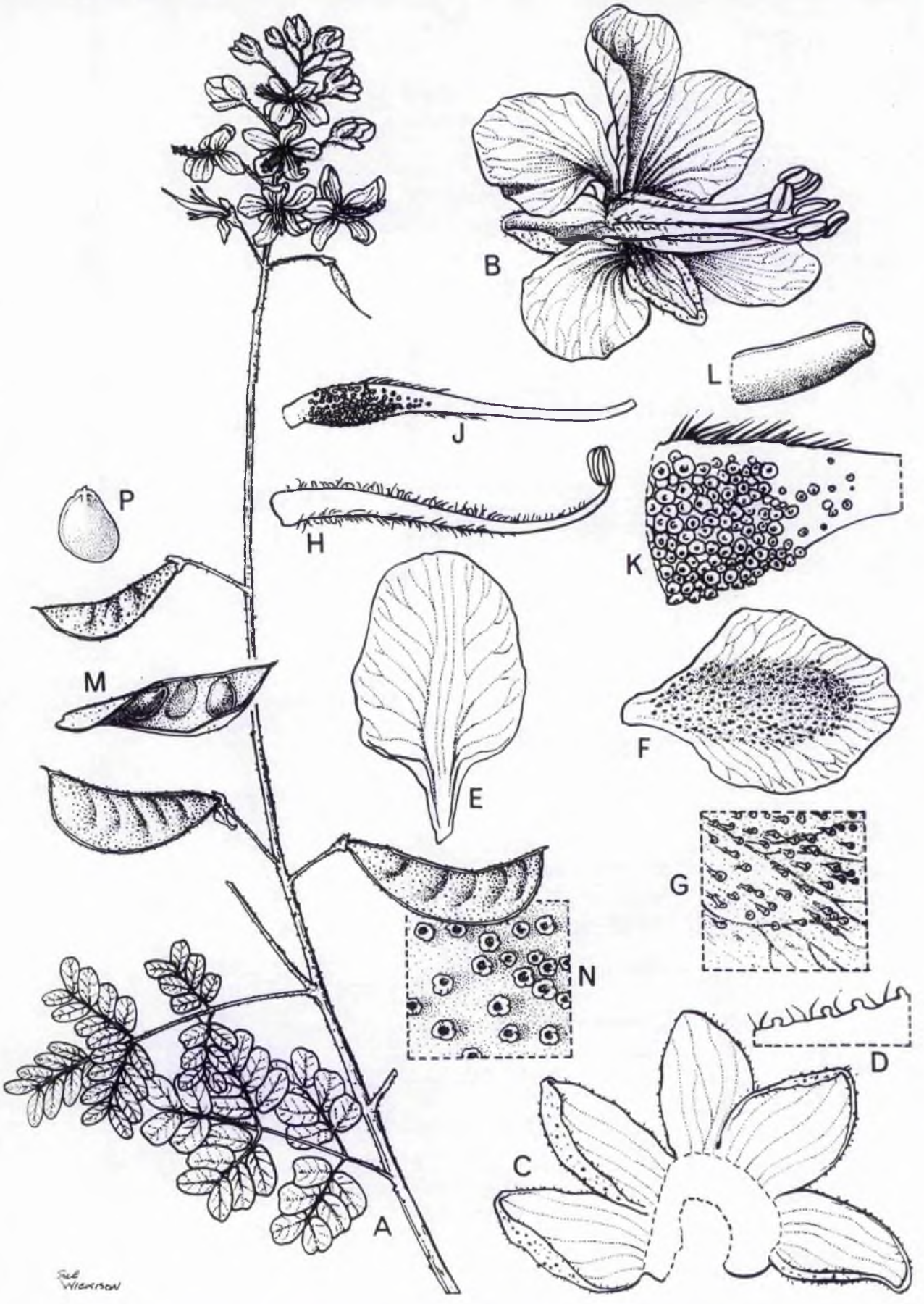
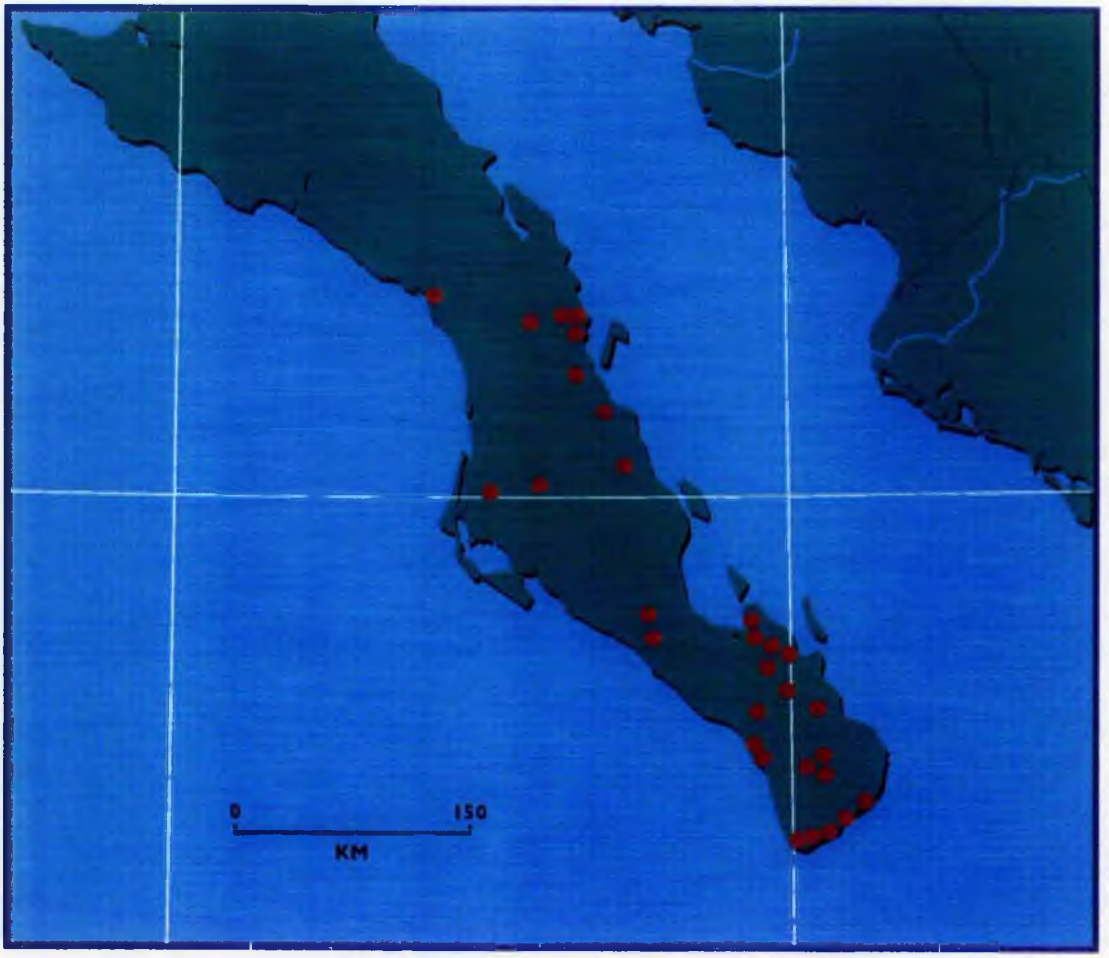


FIG. 16. *Caesalpinia pannosa*. **A** inflorescence and foliage x 1; **B** flower x 4½; **C** calyx opened out x 6; **D** detail of calyx lobe margin x 40; **E** standard petal x 6; **F** dorsal surface of upper lateral petal x 6; **G** detail of glands on upper lateral petal x 40; **H** stamen x 9; **J** gynoecium x 9; **K** gland detail on ovary x 40; **L** stigma x 40; **M** single twisted fruit valve x 1; **N** detail of fruit glands x 40; **P** seed x 1½. **A–G** from *Contreras* 2696, **H–L** from *Daniel* 2439, **M & P** from *Hughes & Styles* 158. Drawn by Sue Wickison.

FIG. 17. *Caesalpinia pannosa*: **A** part inflorescence, cultivated in Texas (*Turner* 88); **B** underside of calyx and glandular dorsal surface of petals, cultivated in Texas (photo.: B.B. Simpson); **C** ovary glands (*Daniel* 2439); **D** petal glands (*Daniel* 2439); **E** glandular fruit (unvouchered); **F** eglandular fruit from same population as **E** (unvouchered). Scale bars = 0.1 mm.

Distribution of *Caesalpinia pannosa* (●) in Baja California



Feb. 1966, *Gould* 11844 (TEX!); 3km NW of San José del Cabo, 22 April 1987, *Hughes & Styles* 158 (K!); Loreto, 19 May 1921, *Johnston* 3774 (K!, NY!); San José del Cabo, 19 Jan. 1928, *Jones* 24018 (F!, NY!); Cacachilla Mountains, 2 Oct. 1930, *Jones* 27257 (NY!); El Carrizal, 25 Feb. 1986, *Léon de la Luz* 994 (MEXU!); 66 km E of Ciudad Insurgentes, track to Agua Verde Bay, 23 Jan. 1992, *Lewis et al.* 2051 (FCME!, FHO!, K!, MEXU!); 79 km NNW of La Paz on road to Constitucion, 22 Jan. 1992, *Lewis et al.* 2049 (FCME!, FHO!, K!, MEXU!, NY!); 65.1 km N of La Paz, highway 1 to Santa Rita, 22 Jan. 1992, *Lewis et al.* 2047 (FCME!, FHO!, K!, MEXU!); 70 km N of Cabo San Lucas, 10 km S of Todos Santos, 21 Jan. 1992, *Lewis et al.* 2045 (FCME!, FHO!, K!, MEXU!, TEX!); just W of San José del Cabo, 21 Jan. 1992, *Lewis et al* 2044 (BM!, FCME!, FHO!, K!, MEXU!, MO!); San José del Cabo, 21 Jan. 1992, *Lewis et al.* 2043 (FCME!, FHO!, K!, MEXU!, NY!); 8 km W of Santiago, 21 Jan. 1992, *Lewis et al.* 2042 (BM!, FCME!, FHO!, K!, MEXU!); 6 km WSW of Miraflores, 20 Jan. 1992, *Lewis et al.* 2041 (BM!, FCME!, FHO!, K!, M!, MEXU!, MO!, NY!, SI!, TEX!, US!); 8 km S of San Pedro, 19 Jan. 1992, *Lewis et al.* 2035 (BM!, FCME!, FHO!, K!, MEXU!, MO!, NY!); La Paz, 19 Jan. 1992, *Lewis et al.* 2033 (BM!, FCME!, FHO!, K!, M!, MEXU!, MO!, NY!, SI!, TEX!, US!); Mpio. La Paz, 31 Aug. 1985, *Luckow et al.* 2838 (TEX!); San Pedro, 13 Jan. 1959, *Moran* 6994 (K!); 2 km below San Bartolo, 20 Jan. 1959, *Moran* 7108 (K!, MEXU!, TEX!); La Paz, 20 Jan. -- 5 Feb. 1890, *Palmer* 114 (F!, K!, MEXU!, NY!); c 3.5 miles E of San Bartolo, 17 Feb. 1960, *Porter* 293 (MEXU!); San José del Cabo, Jan-March 1901, *Purpus* 486 (E!, K!); c 10 miles N of Loreto, 3 Feb. 1977, *Reeder & Reeder* 6779 (MEXU!); Cabo San Lucas, 23 March 1911, *Rose* 16358 (NY!); c 60 km NW of La Paz, 13 Feb. 1972, *Rudd* 3392 (MEXU!); 15 miles S of Rancho Venacio, 21 March 1935,*Schreve* 7192 (F!); c 10 miles W of La Palmilla, 11 March 1967, *Sikes & Babcock* 246 (TEX!); 12.7 miles E of San Carlos docks, 17 Oct. 1981, *Turner & Burgess* 6158 (MEXU!); c 10 miles SW of San José del Cabo, 16 March 1988, *Turner & Turner* 15793 (TEX!); 17--18 miles SW of La Paz, 17 March 1974, *Webster* 19524 (MEXU!); c 23 miles NW of La Paz, 19 March 1974, *Webster* 19561 (LL!, MEXU!, MO!); 4 miles S of Guadalupe, 21 March 1935, *Whitehead* 839 (DS, photo MEXU!); 10 miles SE of La Paz, 1 Dec. 1959, *Wiggins* 15688 (K!, TEX!); 10.3 miles W of La Paz, 31 Dec. 1958, *Wiggins* 14605 (K!, MEXU!, TEX!); 0.6 miles N of Aripes, 3 Jan. 1959, *Wiggins* 14670 (K!, MEXU!); 37 miles N of Santo Domingo, 18 Dec. 1959, *Wiggins & Ernst* 577 (MEXU!); nr. Punta Santo Domingo, 21 Oct. 1962, *Wiggins & Wiggins* 18109 (MEXU!); 3.5 miles S of Rancho Cadaje, *Wiggins* 15202 (K!); 5.5 miles E of La Paz, 10 Dec. 1959, *Wiggins et al.* 444 (MEXU!); Cabo San Lucas, Aug. 1859 -- Jan. 1860, *Xantus* 28 (K!); *Xantus* 29 (lectotype GH!, isolectotype NY!).

ECOLOGY. Open cactus thorn scrub, open sandy washes and plains near the sea to high rocky canyon walls and hillsides, 10--300(--700) m.

PHENOLOGY. Flowering and fruiting from August to April, main flowering late December to March.

VERNACULAR NAME. "Palo estaca".

NOTES. *Caesalpinia pannosa* is a polymorphic species varying greatly in stature, indumentum and gland density. Robust, virtually glabrous forms and squat, contorted, densely pubescent forms intergrade. *C. arenosa, C. californica* and *C. pannosa* are here considered to belong to one variable species. Fruits can be eglandular or densely glandular on plants of one small population. (Fig. 17E & F). Densely pubescent plants usually lack glands on most parts (except petals) or glands are sparse. Gentry 4365 is a particularly pubescent form with densely hairy stems and foliage. Even when mature plants have pubescent foliage the seedlings of these are totally glabrous (e.g. *Lewis et al.* 2051). *Caesalpinia pannosa*, endemic to Baja California belongs to a small group of taxa related to *C. mexicana*, a species essentially of eastern Mexico. *C. standleyi* in western Mexico is somewhat intermediate. A detailed population survey of *C. pannosa* in 1992 confirmed the necessity for the synonymy given here.

In the protologue of *C. pannosa*, Brandegee (1889) gives San Jorge,Comondú as the collection locality but the putative type from UC was collected by Brandegee at San Gregorio. I have been unable to trace a Brandegee collection from San Jorge or Comondú, even though the species has been collected at both localities by other workers. It is possible that the citation of San Jorge was an error for San Gregorio and Brandegee's collection from the latter essentially fits the protologue of *C. pannosa*. In consequence, *Brandegee* s.n. from San Gregorio has here been selected as the lectotype of *C. pannosa*.

5. **Caesalpinia nelsonii** (*Britton & Rose*) *J.L. Contreras* in PhD thesis, UNAM, Mexico D.F.: 91 (1991). Type: Mexico, Guerrero, between Copala and Juchitango [Juchitan], 9 Feb. 1895, *Nelson* 2303 (holotype US!, isotypes GH!, NY!, photo MEXU).
Poincianella nelsonii Britton & Rose in N. Amer. Fl. 23(5): 331 (1930).

Unarmed shrublet or woody-based perennial herb, 0.3--1.5 m tall; bark greyish with white pustular lenticels, young stems green with white lenticels, stems glabrous, occasionally sparsely stipitate-glandular. *Leaves* bipinnate; stipules? ovate, foliaceous, early caducous; petiole red, 2.4--5 cm long, glabrous or pubescent; rhachis red, 1.5--6.2 cm long, glabrous to pubescent; pinnae in 3(--4) opposite pairs plus a terminal pinna, the pinna petiole longer than the rhachis (the leaflets thus clustered at the distal end of the

pinna axis), a triangular, gland-tipped appendage sometimes present between the pinnae insertions on the upper edge of the leaf rhachis, occasionally additional gland-tipped appendages clustered at the pinnae insertions, leaflets glaucous blue green, with a purplish-red margin, 2--3(--4) opposite pairs per pinna, petiolulate, minute gland-tipped stipellate structures at the base of the pulvinules on the lower surface, narrowly obovate to obovate-elliptic, apex rounded to obtuse, mucronate, terminal leaflets7--17 x 2.5--8.5 mm, median leaflets 6.5--16 x 3--8 mm, both surfaces glabrous to pubescent (occurring in same population); main vein prominent on lower surface, secondary venation brochidodromous, eglandular. *Inflorescence* an axillary or terminal 5.5--20 cm long, c 20--60-flowered, glabrous raceme; bracts ovate-acuminate, c 1.5--3 mm long, margins ragged-ciliate, early caducous; pedicels glossy dark red above, green beneath, (7--)9--14.5 mm long, articulated 1.5--2 mm below calyx, glabrous. *Calyx* tube greenish-yellow strongly suffused pinkish-red, glabrous, persisting to mature fruit after sepal abscission; lower sepal cucullate in bud, 4--8 mm long, other sepals 3.5--7 mm long, all sepals glabrous, the margins ragged-fimbriate. *Corolla* bright yellow, standard petal with inner surface flecked orange, blade suborbicular to subcordate, 6.5 --9 x 6.5--9 mm (including a 1.5--2 mm claw) apex rounded, margin induplicate, stipitate-glandular on outer face, claw margin stipitate-glandular, inner surface sparsely to densely silky pubescent with a thickened, pubescent ridge at its apex; upper lateral petals broadly obovate to suborbicular, 8.5--10 x 5.5--7 mm (including a 1.5--2 mm claw); lower lateral petals obovate, 8--10 x 5.5--6.5 mm (including a 1.5--2 mm claw), all lateral petals with a reddish apical blotch on outer surface, claws sparsely pubescent to glabrous, margins stipitate-glandular. Stamen filaments creamish-green, curved, 8.5--12 mm long, pubescent on basal ½--¾, eglandular; anthers yellow, 1.5 x 0.75 mm. Ovary pubescent, 3--4-ovulate; style arcuate, c 8--10 mm long; stigma a terminal, funnel-shaped, fringed chamber. *Fruit* a chartaceous or coriaceous, elastically dehiscent pod, 4.3--5.7 x 1.4--1.5 cm (including an apical beak of 2--3 mm), the valves twist after dehiscence, puberulous, occasionally with a few, yellow, stipitate pixie-cup glands at the base of young fruits, especially on the basal portion of the suture, (1--)2--4-seeded. *Seeds* broadly ovate to subquadrate, 6--8 x 5--7.5 x 1.25--1.75 mm, yellowish-brown, shiny. *Seedling* germination phaneroepigeal, cotyledons foliaceous, apex rounded, base cordate, tardily caducous, first eophyll pinnate with 4 pairs of opposite leaflets, second eophyll alternate to first, bipinnate with one pair

of opposite pinnae plus a terminal pinna, each with 2--3 pairs of opposite leaflets, hypocotyl glabrous, epicotyl glabrous and very sparsely stipitate-glandular. (Figs. 5M, 18 & 62E, Map 6).

DISTRIBUTION. Mexico, endemic to a small stretch of the Pacific coast on either side of the border between Guerrero and Oaxaca.

MEXICO: Guerrero, c 1.5 km S of Agua Zarca, Mpio. Azoyo, 6 March 1983, *Martinez* 3372 (MBM!, MEXU!); Mpio. Cuajinicuilapa, road Acapulo to Pinotepa, km 190, 23 March 1982, *Martinez* 115 (LL!, MEXU!, MO!); road from Copala to Juchitango [Juchitan], 9 Feb. 1895, *Nelson* 2303 (holotype US!, isotypes GH!, NY!); **Oaxaca**, 7 km N of Pinotepa Nacional, 25 Dec. 1974, *Boege* 3325 (MEXU!); Pinotepa Nacional, April 1844 (& May 1845), *Galeotti* s.n. (BR!); c 6--8 km NW of Pinotepa Nacional on highway 125 to Putla, 25 March 1989, *Lewis et al.* 1794 (BR!, CR!, FCME!, FHO!, K!, M!, MEXU!, MO!, NY!, RB!, US!); N of Jicayán, Jamiltepec, 12 May 1972, *MacDougall* H427 (NY!); 12 km N of Santiago Pinotepa towards Putla de Guerrero, 26 Feb. 1992, *MacQueen* 466 (EAP, FHO, K!, MEXU); 7 km SE of Jamiltepec, 27 June 1977, *Sousa et al.* 7666 (MEXU!); 16 km NW of Pinotepa Nacional, 9 Feb. 1976, *Sousa et al.* 5203 (MEXU!, US!); 2 km S of Pinotepa Nacional, 18 April 1976, *Sousa et al.* 5512 (MEXU!); 6 km SE of San Sebastian Ixcapa, 27 June 1979, *Sousa et al.* 10582 (MEXU!); 7 km NW of Pinotepa Nacional, 9 Feb. 1976, *Sousa et al.* 5193 (MEXU!, US!); 24 km NW of Pinotepa Nacional, 9 Feb. 1976, *Sousa et al.* 5210 (MEXU!); Pinotepa Nacional, 7 Dec. 1978, *Sousa & Zarate* 9912 (MEXU!); 21 km NW of Pinotepa Nacional, 17 April 1976, *Sousa et al.* 5498 (MEXU!); 2 km SE of Pinotepa Nacional, 5 Feb. 1977, *Sousa et al.* 7059 (LL!, MEXU!); route to San Agustin Chayuco, 2 km from turn off from Pinotepa Nacional to Puerto Escondido road, 6 April 1982, *Tenorio & Torres* 214 (MEXU!); 5 km NW of Pinotepa Nacional, 9 April 1982, *Tenorio & Torres* 243 (MBM!, MEXU!); without locality or date, *Jurgensen* s.n. (K!).

ECOLOGY. Scrubland, open disturbed woodland, roadsides, 100--500 m.

PHENOLOGY. Flowering and fruiting from late December to May with fruits persisting into June.

VERNACULAR NAME. "Yuca-perichenche gitanilla".

NOTES. Glabrous and pubescent forms are to be found in the same population (e.g. *Lewis* 1794). The species belongs to the *C. mexicana* group.

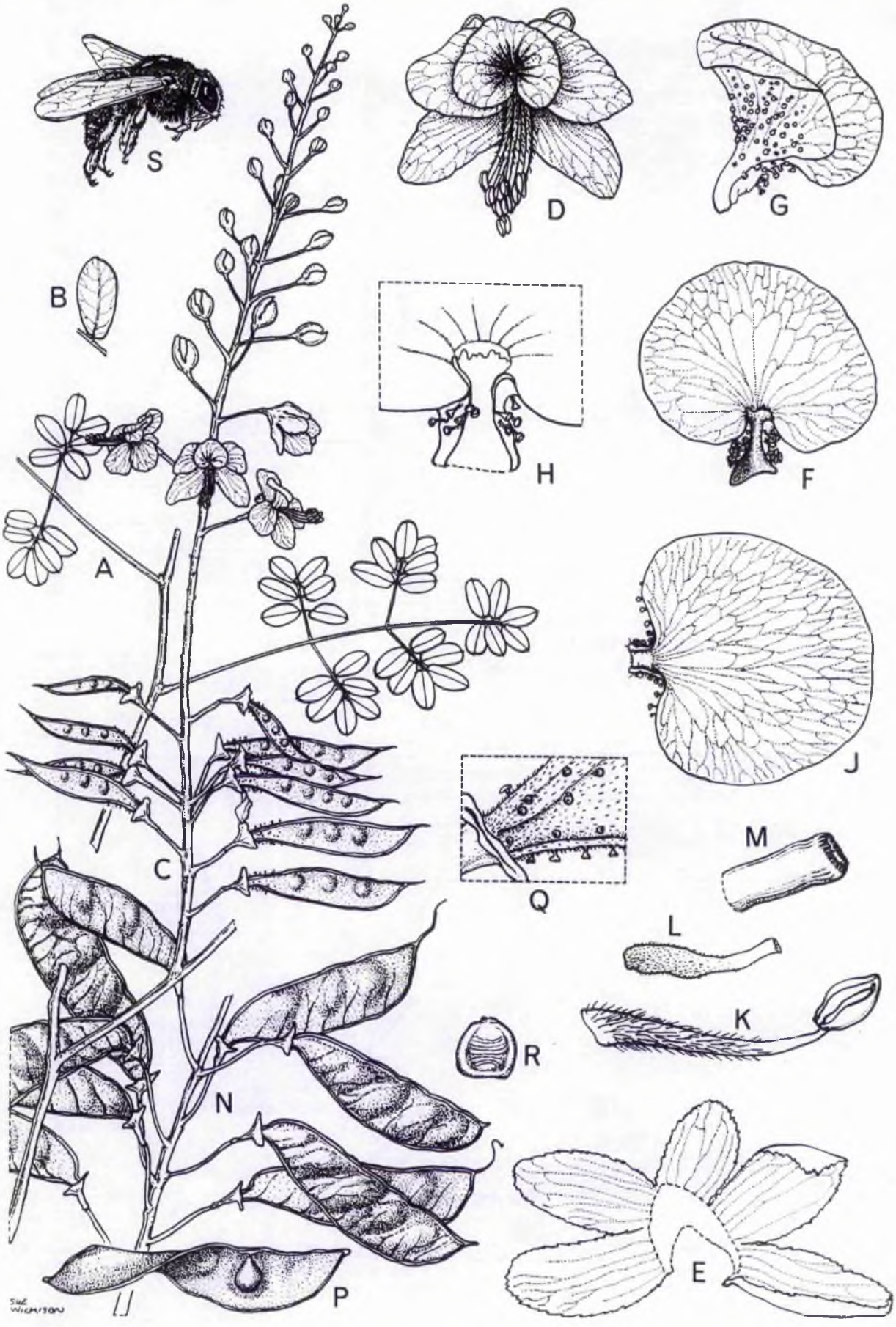


FIG. 18. *Caesalpinia nelsonii*. **A** foliage x 1; **B** median leaflet undersurface x 1½; **C** inflorescence x 1; **D** flower x 6; **E** calyx opened out x 6; **F** standard petal front view x 9; **G** standard petal side view x 9; **H** detail of standard claw x 16; **J** upper lateral petal x 9; **K** stamen x 9; **L** gynoecium x 9; **M** stigma x 30; **N** part infructescence x 1; **P** single twisted fruit valve x 1; **Q** glands on developing ovary x 6; **R** seed x 1½; **S** pollinator – *Xylocopa* sp. All from *Lewis et al.* 1794. Drawn by Sue Wickison.

6. **Caesalpinia standleyi** (*Britton & Rose*) *Standley* in Publ. Field Mus. Nat. Hist. Chicago, Bot. Series 11(5): 159 (1936). Type: Mexico: Nayarit, Acaponeta, 9 April 1910, *Rose et al.* 14190 (holotype NY!).
Poincianella standleyi Britton & Rose in N. Amer. Fl. 23(5): 330 (1930).

Unarmed multiple-stemmed shrub to small tree, 0.5--3.5 m tall, main stems c 2--3 cm in diam.; bark grey with prominent lenticels; whole plant glabrous to moderately pubescent. *Leaves* bipinnate; stipules ovate-orbicular, 2--5 mm long, pubescent; petiole 2--4.8 cm long, glabrous or sparsely pubescent, very sparsely glandular near base; rhachis 4.3--10 cm long, glabrous to moderately pubescent, gland-tipped appendages at pinnae insertions; pinnae in 3--6 opposite pairs plus a terminal pinna; leaflets in 2--5 opposite pairs, petiolulate, discolorous (darker above), obovate, oblanceolate to oblong-elliptic, apices rounded to obtuse to apiculate with a minute glandular mucro, margins revolute, terminal leaflets 10--26 x 5.5--13 mm, medians 8--21 x 5.5--11 mm, both surfaces glabrous to densely pubescent; main vein prominent on lower surface, secondary veins brochidodromous; leaflet blades eglandular, minute gland-tipped appendages at base of petiolules on lower surface. *Inflorescence* a 25--30 cm long, lax, multi-flowered axillary or terminal raceme or shorter, compact terminal panicle; rhachis glabrous to densely pubescent; bracts ovate-lanceolate-cuspidate with a long tail-like, often curled, apex, 3--4 mm long, glabrous to densely pubescent, margin fimbriate, caducous; pedicels (7--)11--16 mm long, glabrous to sparsely pubescent, articulated exactly below or 1.5--2 mm below calyx. *Calyx* upper and lateral lobes 5--6 mm long, glabrous to moderately pubescent, lower lobe 7--8 mm long. *Corolla* yellow; standard petal flecked or spotted red or orange, the lateral petals usually with an apical red flash on outer surface, standard blade depressed-orbicular to subcordate, 8--8.5 x 8--8.5 mm (including a 1.5--2 mm claw), dorsal surface densely glandular with sessile or very short-stalked mushroom-shaped glands, claw thickened, inner surface pubescent, margins pubescent and stipitate-glandular, a pubescent or glabrescent, dentate, thickened ridge of tissue at claw apex; upper lateral petals orbicular to ovate-elliptic, 9--11 x 6--11.5 mm (including a 1--1.5 mm claw), a few sessile, mushroom-shaped glands on dorsal surface of blade base, basal $^1/_3$ --$^1/_2$ of blade margin glandular, claw margin stipitate-glandular, inner surface sparsely pubescent with or without a minute, central, pubescent appendage; lower lateral petals obovate to narowly

obovate-elliptic, 9--12 x 4.5--7 mm (including a 1--2 mm claw), a few glands on dorsal surface of blade base and basal $^1/_3$--$^1/_2$ of blade margin, claw margin stipitate-glandular, inner surface glabrous. Stamen filaments 9--13 mm long, densely spreading pubescent on basal $^1/_2$--$^3/_4$ or for entire length; anthers 1.5 x 0.75 mm. Ovary moderately to densely pubescent, glandular; style 9 mm long; stigma a terminal, tubular to slightly flared, fringed chamber. *Pod* subligneous, elastically dehiscent, 4.1--5.5 x 1.5--1.6 cm (including a 1 mm beak and 2 mm stipe), glabrous to moderately pubescent (the hairs most evident on the suture), 2--3-seeded. (Map. 5).

DISTRIBUTION. Mexico: Sinaloa, Nayarit and Jalisco.

MEXICO: Sinaloa, Mazatlan, Dec. 1894, *Lamb* 341 (K!, NY!); Arroyo Navarrete, without date *Ortega* 6007 (K!); **Nayarit**, 24 km S of Tepic on rd. to Mazatlan, 6 March 1990, *Contreras* 2745 (K!); 3 km SW of Acaponeta, rd. Tepic to Mazatlan, 25 Feb. 1990, *Contreras* 2694 (K!); Acaponeta, 26 Feb. 1927, *Jones* 23019 (F!); *Jones* 23010 (F!, NY!); 11 km S of Acaponeta on rd. to Tepic, 2 Feb. 1992, *Lewis et al.* 2078 (FCME!, FHO!, K!, MEXU!); Acaponeta, 9 April 1910, *Rose et al.* 14190 (holotype NY!); **Jalisco**, Sierra Madre Occidental, NW of San Sebastian, Las Mesitas, La Junta, 16 March 1927, *Mexia* 1887 (F!, NY!).

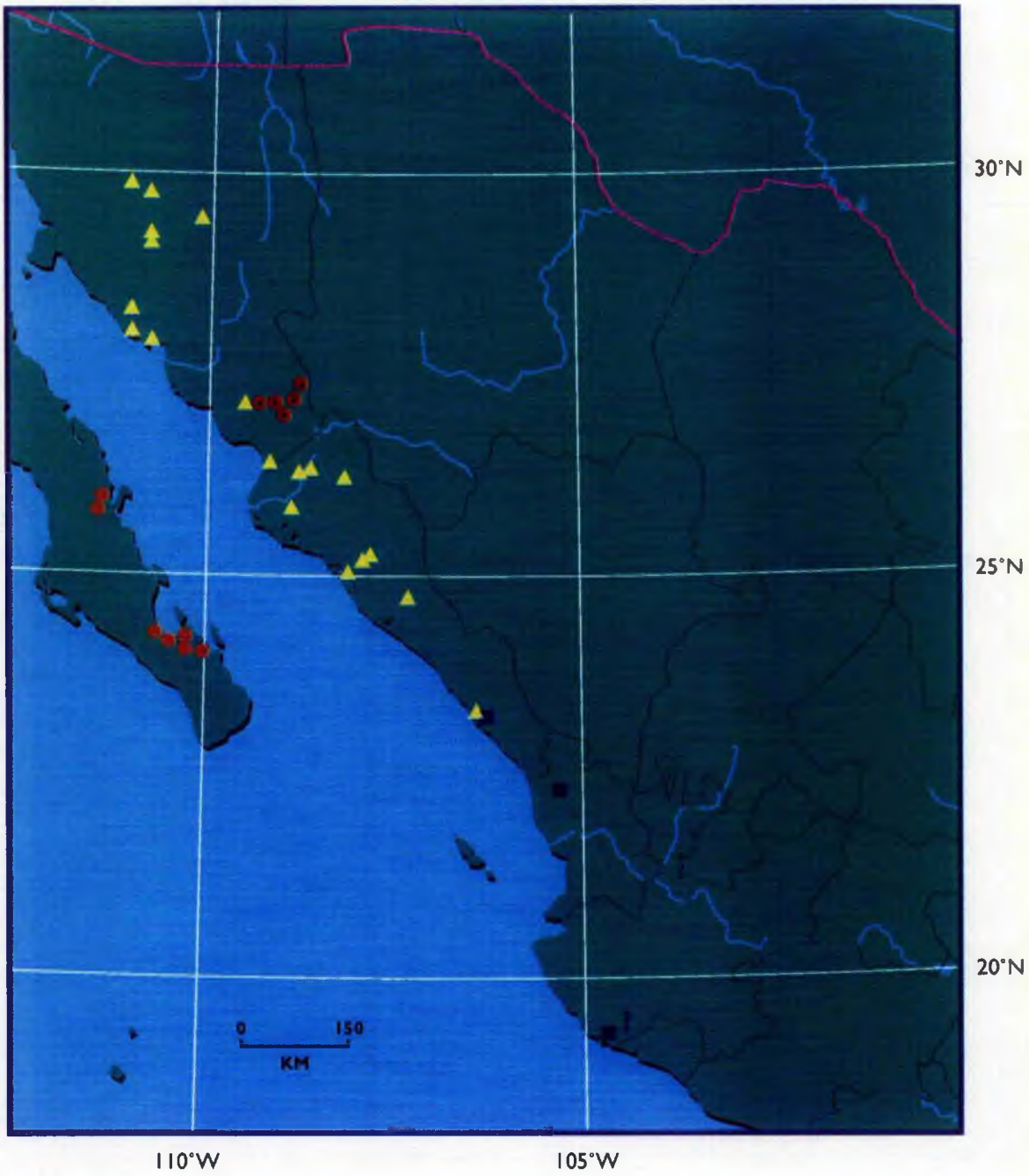
ECOLOGY. Deciduous tropical woodland, often in highly degraded sites, 20--1700 m.

PHENOLOGY. Flowering from December to March, fruiting from February to April.

VERNACULAR NAME. "Viche" (Sinaloa).

NOTES. The short acuminate bracts and the dentate thickened ridge at the claw apex of the standard petal appear to be consistent and diagnostic for *C. standleyi*, but the *Caesalpinia standleyi* 'complex' displays other morphological characters that intergrade with *C. acapulcensis* (to the south) and the two species may hybridise (e.g. *Rico and Windsor-Shaw* 833, from Jalisco, could be of hybrid origin). The complex also intergrades morphologically with *C. mexicana* from eastern Mexico and *C. caladenia* from Sonora. *Miller et al.* 383 collected just S of La Huerta in Jalisco is probably a specimen of *C. standleyi* but cannot be placed here with certainty. *Lewis et al.* 2077, collected 55 km N of Mazatlan in Sinaloa is another specimen of possible hybrid origin possessing elements of *C. caladenia* and *C. standleyi*.

Distribution of *Caesalpinia caladenia* (●) *C. palmeri* (△) *C. placida* (●) and *C. standleyi* (■) in Western Mexico and Baja California



Caesalpinia collections from southern Sinaloa, Nayarit and western Jalisco that fall into the *C. standleyi* 'complex' all suggest that geographically this area is critical to understanding patterns of speciation in a closely related group of taxa that includes *C. caladenia, C. acapulcensis, C. standleyi, C. palmeri* and *C. mexicana*. More collections and a detailed field survey are needed in order to unravel the taxonomy. Hybridization experiments are also needed to look at interfertility between these closely related species. The trans-Mexican volcanic belt includes southern Jalisco and Nayarit (Ferrusquía-Villafranca, 1993) thus coinciding geologically with an apparent genetic plasticity in western Mexican *Caesalpinia* taxa. This apparent relationship requires an in depth investigation.

7. **Caesalpinia acapulcensis** *Standley* in Contribs. U.S. Nat. Herb. 20: 213 (1919). Type: Mexico, Guerrero, vicinity of Acapulco, Oct. 1894 - March 1895, *Palmer* 505 (holotype US!, isotypes F!, GH!, K!, MEXU!, NY!).
   Poincianella acapulcensis (Standley) Britton & Rose in N. Amer. Fl. 23(5): 329 (1930).

Unarmed shrub to single or multiple-stemmed small tree, 2.5--7 m tall; bark greyish-pale brown with white lenticels; stems pubescent and densely stipitate-glandular. *Leaves* bipinnate; petiole 1.8--4 cm long, glabrous or less frequently pubescent, a few stipitate glands at base; rhachis 3--5 cm long, glabrous or pubescent; pinnae in 2--3 opposite pairs plus a terminal pinna; leaflets in 2--3 opposite pairs, elliptic to broadly ovate, apex rounded to obtuse, base asymmetric, 1.8--4.9 x 1.4--2.5 cm, both surfaces glabrous or pubescent; secondary veins brochidodromous, evident on both surfaces; blades eglandular, gland-tipped appendages between and below pinnae insertions. *Inflorescence* a 25--60(--multi)-flowered terminal raceme or panicle up to c 30 cm long, puberulous, densely stipitate-glandular or eglandular but the trichomes plumose; bracts dark reddish-brown, ovate, acute to acuminate, 4.5--7 mm long, puberulous, densely stipitate-glandular or eglandular, subpersistent; pedicels 6--10 mm long, puberulous, densely stipitate-glandular, articulated 1--2 mm below calyx. *Calyx* with upper and lateral lobes 6.5--7 mm long, surfaces and margin puberulous and stipitate-glandular, lower lobe 7--7.5 mm long,

sometimes splitting slightly at apex. *Corolla* yellow; standard petal faintly spotted reddish-orange, blade ± orbicular, 9--12 x 7--10 mm (including a 2--3 mm claw), upturned base sometimes pubescent, thickened, stipitate-glandular, claw thickened, grooved, its margin stipitate-glandular, apex with a thickened ± glabrous ridge, inner face pubescent, a small tuft of hairs on each margin at base; upper lateral petals orbicular to depressed-orbicular, 10--13 x 6.5--12 mm (including a 2--3 mm claw), base of blade and top of claw margin thickened, inrolled and glandular, claw hairy at base, margin stipitate-glandular, inner surface pubescent or with a minute, centrally positioned, hairy appendage; lower lateral petals obovate, oblanceolate to suborbicular, 11--13.5 x 6--9 mm (including a 2.5--3 mm claw), one side of claw thickened and inrolled, both margins stipitate-glandular, sparsely pubescent or glabrous at base. Stamen filaments 12--16 mm long, densely white pubescent on lower $^1/_2$--$^2/_3$; anthers 1.5 x 1 mm. Ovary pubescent, densely stipitate-glandular; style 8--14 mm long, pubescent and glandular on lower $^1/_3$, or pubescent almost to apex; stigma a terminal, tubular, fringed chamber. *Pod* subligneous, elastically dehiscent, 4.5--9.2 x 1.2--2.2 cm, puberulous, the hairs most evident on the margins, glabrescent, densely stipitate-glandular or eglandular but for a few glands at base on suture, 2--4-seeded. *Seeds* pale brown-fawn, ovate, 8 x 8 x 2 mm. (Figs. **19** & 21C-E, Map 6).

DISTRIBUTION. Mexico: Jalisco, Colima, Michoacan and Guerrero.

MEXICO: Jalisco, Mpio. La Huerta, Rancho Cuixmala, 13 Jan. 1991, *Lott et al.* 3205 (K!); Est. Biologia Chamela, 8 Feb. 1990, *Rico & Windsor-Shaw* 836 (K!, MEXU!); **Colima** Manzanillo, ?1890, Feb. 1891 *Palmer* 'F' (K!, NY!); **Michoacan**, Distr. Coalcoman, nr. Aquila, Nov.-Dec. 1941, *Hinton et al.* 16198 (K!); 5--10 km W of Huahua on main coastal hwy. W from Playa Azul, 19 March 1985, *Hughes* 628 (K!, MEXU!); San Juan de Lima, S of Coahuayana, 14 March 1965, *McVaugh* 22987 (NY!); **Guerrero**, c 2 mi. E of Acapulco, Playa Hornita, 3 Jan. 1944, *Barkley* 14106 (MEXU!, TEX!); Zihuataneyo, 20 Dec. 1970, *Boege* 1622 (MEXU!); 10 km W of San Juan Tetelcingo, 19 Feb. 1986, *Contreras* 1846 (K!); *Contreras* 1842 (K!); *Contreras* 1844 (MEXU!); Zihuatanejo, 31 Jan. 1977, *Germán et al.* 224 (MEXU!, NY!); 26 km SE of Petatlán, 20 Dec. 1977, *Grether & Quero* 895 (MEXU!); Distr. Galeana, Atoyac, 30 Nov. 1937, *Hinton et al.* 10991 (K!, LL!, NY!); c 11 km N of Acapulco, 22 Jan. 1982, *Lorence et al.* 3825 (F!, MEXU!); 49.8 km N of La Union, 13 Feb. 1992, *MacQueen et al.* 447 (EAP!, FHO!, K!, MEXU!); 32 km E of Acapulco, 23 March 1982, *Martínez & Téllez* 89 (LL!, MEXU!); Sierra Madre del Sur, N of Rio Balsas, Distr. Adama, 12 Nov. 1937, *Mexia* 8798 (F!, K!, NY!); Acapulco and vicinity, Oct. 1894 - March 1895, *Palmer* 505 (holotype US!, isotypes F!, GH!, K!, MEXU!, NY!).

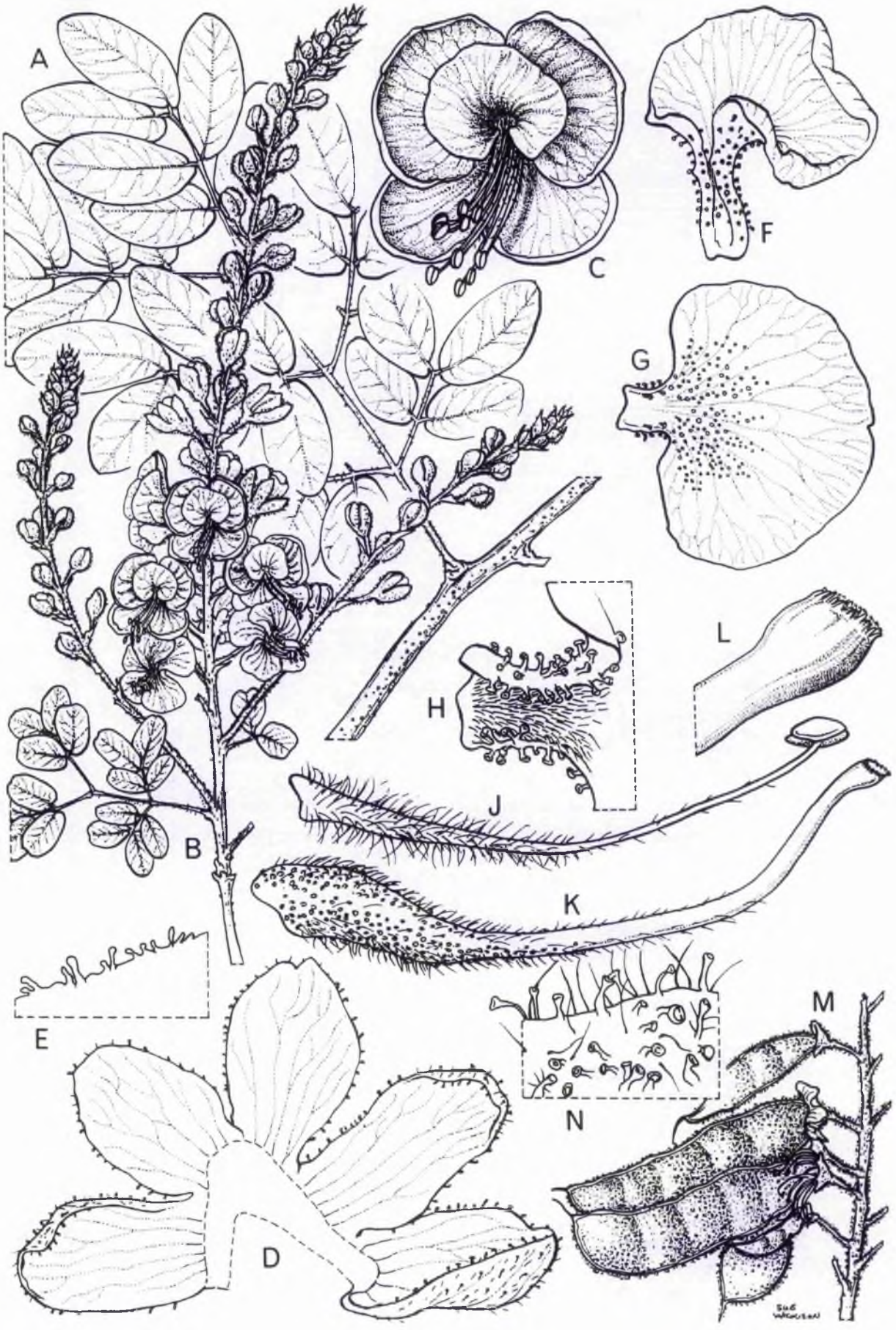
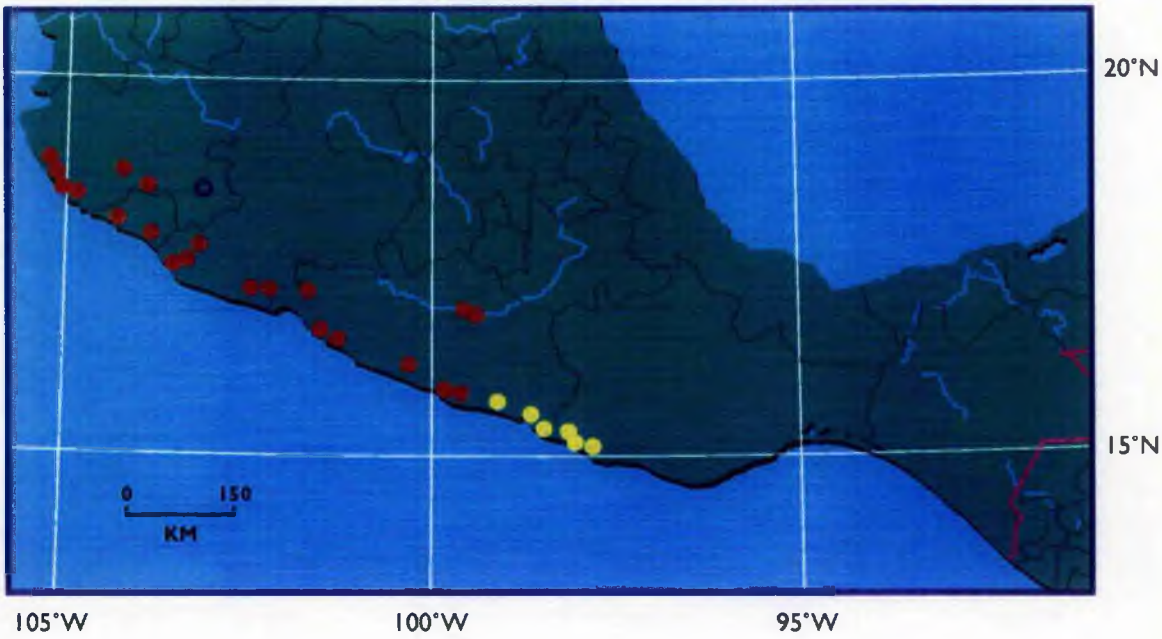


FIG. 19. *Caesalpinia acapulcensis*. **A** part bipinnate leaf x 1; **B** inflorescence x 1; **C** flower x 3; **D** calyx opened out x 6; **E** calyx lobe margin x 18; **F** standard petal x 6; **G** outer surface of upper lateral petal x 6; **H** inner surface of upper lateral petal claw x 12; **J** stamen x 9; **K** gynoecium x 9; **L** stigma x 30; **M** fruits x 1; **N** detail of fruit glands x 30. **A–C, M & N** from *Núñez* 584, **D–L** from *McVaugh* 22987. Drawn by Sue Wickison.

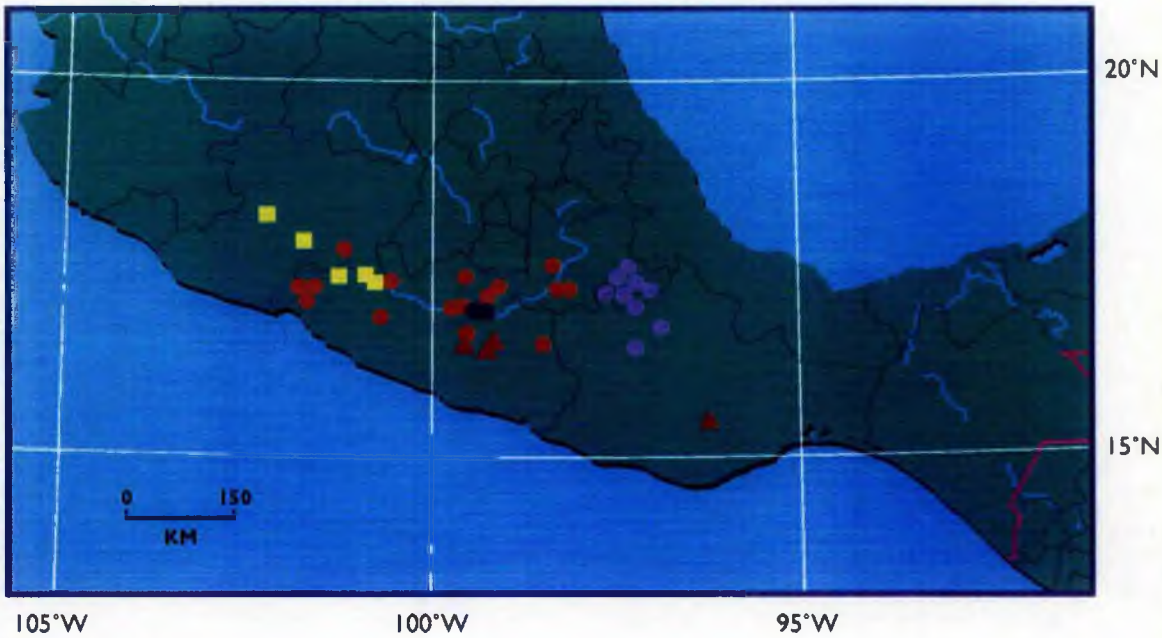
Map 6

Distribution of *Caesalpinia acapulcensis* (●) *C. nelsonii* (○) and *Poincianella robinsoniana* (o) in Mexico



Map 7

Distribution of *Caesalpinia epifanioi* (●) *C. hintonii* (●) *C. laxa* (▲) *C. macvaughii* (□) *and C. melanadenia* (●) in Mexico



ECOLOGY. Low deciduous forest, especially in disturbed areas; rocky slopes near the sea and beach thickets, 10--650 m (?--1000 m).

PHENOLOGY. Flowering from November to March, fruiting December to March.

VERNACULAR NAME. "Cuasillo" (Guerrero).

NOTES. Several characters of *C. acapulcensis* intergrade with those of closely related *C. caladenia* from Sonora and *C. standleyi* from Sinaloa, Jalisco and Nayarit. It is possible that *C. acapulcensis* is just an infraspecific taxon of *C. caladenia*; Contreras (1991) considered the two to be synonymous. *C. caladenia* does, however, differ in having calyx lobes which tend to be narrower, the apical ridge on the standard claw densely pubescent, the ovary densely sericeous, the bracts larger and white puberulous, the inflorescence a lax raceme and the leaflets smaller. Hughes (collection 628) reports that *C. acapulcensis* is frequent along the coast in Michoacan. Higher altitude populations (500-650 m) tend to have smaller flowers and fruits. *Hughes & Styles* 142, a fruiting specimen, has the leaf formula of *C. standleyi* but fruits that better match *C. acapulcensis*. McVaugh (1987) reports a form of *C. caladenia* from the Rio Corcovado with both surfaces of the leaflets softly pilose. This description equates with the Hughes and Styles collection from the same locality; it is not *C. caladenia*. *Lott et al.* 3297 from Jalisco is essentially *C. acapulcensis* but with bracts of *C. standleyi* and may be a hybrid between the two. *McQueen et al.* 406 has some leaflets with the lower surface pubescent, the inflorescence lacks stipitate glands but is covered in plumose trichomes, the fruits are eglandular and the bracteoles are smaller, narrower and more acuminate than found on *C. acapulcensis sens. strict.* However, *C. acapulcensis* has glandular and ± eglandular forms, especially with reference to fruits and inflorescence rhachides. The Kew duplicate of *Palmer* 505, an isotype of *C. acapulcensis*, has the bottom specimen stipitate-glandular and the top one eglandular but with a dense covering of plumose trichomes (exactly matching *MacQueen et al.* 406). It is to be assumed that these are from different plants of the same population. *McQueen et al.* 430, from Guerrero, has the bracts of *C. acapulcensis* but is otherwise difficult to separate from *C. caladenia*, other than by its collection locality. Several collections seen in MEXU during the early part of this study need to be restudied to confirm their identification as *C. acapulcensis*. They are not cited in this treatment. Standley (1919), when describing *C. caladenia*, assigned two Palmer

collections from Colima to that species; I have seen the K and NY specimens of Palmer 'F' which better matches *C. acapulcensis*.

8. **Caesalpinia caladenia** *Standley* in Contribs. U.S. Nat. Herb. 20: 214 (1919). Type: Mexico, Sonora, c 5 miles below Minas Nuevas, 12 March 1910, *Rose et al.* 12660 (holotype US!, isotype NY!).
   Poincianella caladenia (Standley) Britton & Rose in N. Amer. Fl. 23(5): 329 (1930).

Unarmed shrub to single or multiple-stemmed slender tree, 3.5--6 m tall, crown an inverted cone shape, much branched, main trunks 5--20 cm in diam.; bark grey with dense white lenticels; stems glabrous. *Leaves* bipinnate, arising from woody brachyblasts; stipules ovate-elliptic, oblong-elliptic to orbicular-concave, 4--9 mm long, apex obtuse to acute, base ± cordate, silky pubescent, margin ciliolate-fimbriate; petiole 3--5.7 cm long, on young leaves pubescent and glandular-stipitate near the base, glabrescent, on mature leaves glabrous; rhachis 2--7 cm long, glabrous; pinnae in 2--3 opposite pairs plus a terminal pinna; leaflets in 2--4 opposite pairs, terminal leaflets elliptic to ovate-elliptic, 10--25 x 5--15 mm, apex rounded, obtuse or shallowly emarginate, occasionally apiculate and gland-tipped, median leaflets obovate, elliptic-subrhomboid, oblong-elliptic to ovate-elliptic, 9--22 x 5--14 mm, all leaflets with both surfaces glabrous, main vein prominent on lower surface, secondary veins brochidodromous, blades eglandular, short gland-tipped appendages at pinnae insertions and base of leaflet petiolule. *Inflorescence* a sessile or short-pedunculate, 25--60-flowered, axillary or terminal raceme or terminal panicle, sometimes arising from woody brachyblasts, the rhachis and pedicels densely pubescent and stipitate-glandular, the pixie-cup glands with hairy stalks; bracts ovate-lanceolate to ovate, 6--11 mm long, outer surface densely pubescent and stipitate-glandular, margin glandular, subpersistent; pedicels 10--14 mm long, articulated 1--3 mm below calyx. *Calyx* with upper and lateral lobes 6--7 mm long, densely pubescent, margin glandular, lower lobe cucullate-imbricate, 8--8.5 mm long. *Corolla* yellow; the standard petal without markings or streaked orange near base, blade cordate or orbicular 9--10 x 8 mm (including a 1--2.5 mm claw), base folded upwards, basal $^1/_3$--$^1/_2$ of dorsal face glandular, claw apex with a thickened densely pubescent ridge or with two densely sericeous

triangular appendages, margin pubescent and stipitate-glandular; upper lateral petals elliptic-orbicular, 9--11 x 7.5--9 mm (including a 1--2 mm claw), blade outer surface sparsely glandular on basal $^1/_4$--$^1/_3$, margin at base with long stipitate-glands, claw apex with long stipitate glands at margin and small tuft of hairs on inner surface, glandular and pubescent at base; lower lateral petals elliptic-obovate, 11--12 x 5.5--6.5 mm (including a 1--2.5 mm claw), outer surface of blade glandular on basal $^1/_4$--$^1/_3$, claw margin stipitate-glandular, glabrous, sometimes a few sparse hairs on inner surface. Stamen filaments 10--12 mm long, pubescent for entire length or only on basal ½; anthers pale orange when fresh, 1.5--2 x 0.75--1 mm. Ovary densely silky pubescent, the pubescence sometimes obscuring the dense stipitate pixie-cup glands, the gland stalks hairy, 4-ovulate; style 9 mm long, basal $^1/_3$--$^1/_2$ densely pubescent, hairs becoming sparse towards apex; stigma a terminal, ± flared, fringed chamber. *Pod* subligneous, elastically dehiscent, 7.5--8.4 x 1.8 cm, pubescent, stipitate-glandular, 2--3-seeded. *Seeds* depressed-elliptic to subcordate, 8--9.5 x 10.5--11.5 x 1.5 mm. (Figs. 1C, **20**, & 21A, Map 5).

DISTRIBUTION. Apparently endemic to Sonora, Mexico.

MEXICO: Sonora, 7 km NE of Minas Nuevas, 3 March 1990, *Contreras* 2728 (K!); *Contreras* 2729 (K!); Ejido Colonia Francisco Villa, km 27, road Alamos to Navojoa, 4 March 1990, *Contreras* 2731 (K!); San Bernado, Rio Mayo, 1 March 1935, *Gentry* 1378 (in part) (F!, K!, MEXU!); Rio Mayo, Alamos, 5 Feb. 1937, *Gentry* 2989 (F!, K!); 29 km from Navojoa on road to Alamos, 31 Jan. 1992, *Lewis et al.* 2072 (FCME!, FHO!, K!, MEXU!); 29.5 km from Navojoa on road to Alamos, 31 Jan. 1992, *Lewis et al.* 2073 (FCME!, FHO!, K!, MEXU!); *Lewis et al.* 2074 (FCME!, K!, MEXU!); c 5 mi. below Minas Nuevas, 12 March 1910, *Rose et al.* 12660 (holotype US!, photo MEXU!, isotype NY!); 14 mi. W of Alamos on rd. to Navojoa, 4 April 1982, *Sanders et al.* 2592 (TEX!).

ECOLOGY. Deciduous thorn forest on limestone, 220--410 m.

PHENOLOGY. Flowering January to April, fruiting March and April.

VERNACULAR NAME. "Margarita", "Wetapochi" (both names cited on Gentry 1378, a mixed collection of *C. caladenia* and *C. palmeri*).

NOTES. *C. caladenia* is closely related to *C. acapulcensis*, as stated by Standley (1919), the author of both names, and several characters of both species intergrade.

FIG. 20. *Caesalpinia caladenia*. **A** part bipinnate leaf x 1; **B** median leaflet undersurface x 1½; **C** apical leaflet undersurface x 1½; **D** median leaflet undersurface x 1½; **E** section of branch bark x 1½; **F** inflorescence x 1; **G** pedicel detail x 15; **H** bract x 3; **J** flower x 1½; **K** calyx opened out x 2¼; **L** standard petal x 3; **M** l.s. standard petal base x 9; **N** upper lateral petal x 3; **P** lower lateral petal x 3; **Q** stamen x 4½; **R** gynoecium x 4½; **S** stigma x 30; **T** fruit x 1. **A & B** from *Lewis et al.* 2072, **E** from *Contreras* 2729, **F** from *Lewis et al.* 2073, **T** from *Contreras* 2731, the rest from Lewis et al. 2074. Drawn by Eleanor Catherine.

FIG. 21. *Caesalpinia caladenia*: **A** flower (*Lewis et al.* 2074); *C. palmeri:* **B** inflorescence (*Lewis et al.* 2063); *C. aff. acapulcensis*: **C** fruits (*MacQueen et al.* 406); **D** inflorescence (*MacQueen et al.* 406); **E** dehisced fruits (*MacQueen et al.* 406); *C. mexicana*: **F** flowers (*Hughes et al.* 1609, photo.: C.E. Hughes).

Standley recognised *C. caladenia* as distinct from *C. acapulcensis* by its glandular fruit, larger flowers and smaller, narrower, more numerous leaflets. These are all features that vary, sometimes considerably, within one species. Contreras (1991) placed *C. acapulcensis* in synonymy under *C. caladenia* in his account of *Caesalpinia* for the Mexican state of Guerrero. This was a practical solution to a complicated problem. Nevertheless, *C. caladenia*, apparently endemic to Sonora, does present an overall facies that readily and consistently permits its separation from *C. acapulcensis* in Jalisco, Colima, Michoacan and Guerrero. The Sonoran species has larger bracts with a white pubescence, usually a lax racemose inflorescence and generally smaller leaflets. The bracts of *C. acapulcensis* are smaller, darker and more acute, the inflorescence is often (but not always) a panicle, and the leaflets are usually much larger. However, the situation is further complicated by the intergradation of *C. acapulcensis* with *C. standleyi* and the intergradation of *C. caladenia* and *C. palmeri*. In fact, *Lewis et al.* 2075 from Sonora, is a possible hybrid between *C. caladenia* (usually a small tree) and *C. palmeri* (usually a shrub). The collection has short inflorescences, the standard petal blotched red at its base, the laterals red at the apices, glands on pedicels and inflorescences sparse and the leaflets mostly small, all characters of *C. palmeri*. The material also has some larger leaflets, a dense grey indumentum on the inflorescences, the calyces not strongly suffused purple and the standard petal claw apex with a densely pubescent ridge, all characters of *C. caladenia*. Additional collections of *C. caladenia, C. acapulcensis, C. palmeri* and *C. standleyi* are needed before this group of species can be resolved. In particular, experimental work needs to be undertaken to test the theory that natural hybrids exist.

9. **Caesalpinia palmeri** *S. Wats.* in Proc. Am. Acad. 24: 47 (1889). Type: Mexico, Sonora, Guaymas, June 1887, *Palmer* 70 (holotype US!, isotypes GH!, K!, NY!).
   Poinciana palmeri (S. Wats.) Rose in Contribs. U.S. Nat. Herb. 13: 303 1911).
   Poincianella palmeri (S. Wats.) Britton & Rose in N. Amer. Flora 23(5): 332 (1930).
   Poincianella arida Britton & Rose in N. Amer. Flora 23(5): 332 (1930). Type: Mexico, Sonora, near Hermosillo, 7 March 1910, *Rose et al.* 12508 (holotype NY!).
   Caesalpinia arida (Britton & Rose) Wiggins in Contribs. Dudley Herb. 3(3): 69 (1940).

Unarmed, single or multiple-stemmed open spreading shrub to small tree, 1--3.5 m tall, trunks or main basal stems 1.5--5 cm in diam.; bark on older wood greenish-grey with slightly pustular, white lenticels, bark of young stems black with scattered, white, pustular lenticels; young stems glabrous; leaves and inflorescences arising from short woody brachyblasts. *Leaves* bipinnate; stipules broadly triangular-ovate, thin, scarious, ± persistent; petiole 4--16 mm long; rhachis 0.6--3.9 cm long, glabrous or pubescent; pinnae in 1--4 opposite pairs, plus a terminal pinna, each pinna terminated by a short, caducous mucro; leaflets in 2--4 opposite, subsessile pairs, narrowly elliptic to obovate, apex rounded, base asymmetric, rounded, margins usually ± thicker, terminal leaflets 3--13 x 1.75--7.5 mm, median leaflets 2.5--12 x 1.5--5.5 mm, both surfaces glabrous or pubescent; ± fleshy, venation obscure, the main vein evident as a sunken groove on lower surface, secondary venation brochidodromous; main vein terminating in a glandular tip, leaflet blades eglandular or margin crenulate and glandular (e.g. *Gentry* 7139), gland-tipped minute appendages below leaflet pulvinules and at pinnae insertions on leaf rhachis, sometimes also scattered on petiole. *Inflorescence* a highly reduced terminal, axillary or pseudolateral raceme of 1--15 flowers, these often aggregated into a leafy brachyblast or congested panicle, rhachis, pedicels and calyces densely white spreading pubescent; bracts ovate-lanceolate, acuminate, 2.5--4 mm long, short-pubescent, caducous; pedicel 8--13 mm long, articulated 1--2 mm below calyx; mature buds asymmetric with a truncate base. *Calyx* lower lobe cucullate, 7 mm long, the margin glandular fimbriate, the apex usually splitting, other four lobes 5--6 mm long, the outer surface densely pubescent, inner surface finely pubescent, margins stipitate glandular, all four reflex as the flower opens. *Corolla* bright yellow; standard petal streaked, flecked or veined reddish-orange, its blade orbicular, apex rounded to shallowly emarginate, 8--9 x 6--6.5 mm (including a 2--2.5 mm claw), base of blade folded upwards on either side of claw apex, inner surface of claw pubescent, especially near apex, sometimes two small triangular pubescent appendages at claw apex, claw margin stipitate-glandular, outer surface of blade stipitate-glandular near base and on claw; upper lateral petals broadly triangular-orbicular, apex rounded, 7--10 x 5--8 mm (including a 2--2.5 mm claw), claw margin glandular, inner surface pubescent; lower lateral petals obovate, 8--11 x 4--6 mm (including a 2 mm claw), claw margin glandular, inner surface very sparsely pubescent, all lateral petals with orangish-red

streaks, whole petal fading orange, dorsal surface basally to almost entirely glandular with yellowish glands. Stamen filaments pale yellowish-cream or greenish, c 10 mm long, white pubescent on basal $^{1}/_{2}$--$^{2}/_{3}$, especially on inner surface; anthers pink or purplish-red, 2 x 0.75 mm. Ovary densely pubescent with reddish pixie-cup stipitate glands intermixed; style pinkish-red, c 9 mm long, pubescent and glandular on basal ½; stigma a red, terminal, flared, fringed chamber. *Fruit* an elastically dehiscent, subligneous, falcate, scimitar-shaped pod, characteristically tinged purplish, 3.5--5.5 x 1--1.5 cm, pubescent with short-stalked pin-shaped glands intermixed, valves twist after dehiscence, 2--4-seeded. *Seeds* ovate, subquadrate to subtriangular, 7--9 x 6--8 x 1.5--2 mm, brown or olive-brown, glossy. (Figs. 7M, 21B & 22, Map 5).

DISTRIBUTION. Mexico: Sonora and Sinaloa.

MEXICO: Sonora, near Poza, 11 April 1932, *Abrams* 13281 (F!); 4 miles NW of Tetas de Cabra, Bahia San Carlos, 29 April 1975, *Carter et al.* 75--29 (MEXU!); Bahia San Carlos, 8 Feb. 1940, *Dawson* 1061 (F!); 38 miles S of Hermosillo, 7 March 1978, *Dillon & Rodriguez* 1041 (MO!, NY!); Hermosillo, 7 Nov. 1939, *Drouet et al.* 3498 (F!); 29.2 miles N of Hermosillo, 22 Feb. 1958, *Felger* 2415 & *Lowe* 1615 (MEXU!); Caña Nacapules, c 6 km N of Bahia San Carlos, 9 March 1985, *Felger et al.* 85--584 (TEX!); c 8 miles N of Guaymas, shores of Bahia San Carlos, 19 March 1934, *Ferris* 8720 (NY!); San Bernado, Rio Mayo, 1 March 1935, *Gentry* 1378 in part (F!, K!, MEXU!); near Carbo, 50 miles S of Santa Ana, 20 April 1939, *Gentry* 4464 (K!); Agiabampo, 30 May 1944, *Gentry* 7035 (F!, NY!); Hermosillo, 1 May 1936, *Gentry* 2189 (F!); Guaymas, 15 April 1921, *Johnston* 3104 (K!); 75 km S of Hermosillo on highway 15, 28 Jan. 1992, *Lewis et al.* 2065 (FCME!, FHO!, K!, MEXU!, TEX!); 8 km along road Guaymas to Hermosillo, 27 Jan. 1992, *Lewis et al.* 2063 (BM!, FCME!, FHO!, K!, MEXU!, NY!); same locality and date, *Lewis et al.* 2064 (FCME!, FHO!, K!, MEXU!); 33 miles SE of Navojoa on highway 15, 12 April 1970, *Mahler & Thieret* 6000 (NY!); S of Hermosillo, 20 Feb. 1959, *Miranda* 8939 (MEXU!); Mpio. of Carbo, 10 July 1970, *Norris & Taranto* 12477 (MEXU!); Guaymas, June 1887, *Palmer* 70 (holotype US!, isotypes GH!, K!, NY!); Guaymas, Feb. 1890, *Palmer* 146 (F!, K!, NY!); near Hermosillo, 7 March 1910, *Rose et al.* 12508 (NY!); Hermosillo, 4 March 1910, *Rose et al.* 12380 (F!, NY!); Hermosillo to Guaymas, 4 Dec. 1968, *Rudd* 2088 (MEXU!); Bahia San Carlos, 2 April 1982, *Sanders et al.* 2497 (TEX!); 24 miles S of Benjamin Hill, highway 15, 1 April 1982, *Sanders et al.* 2477 (TEX!); Rancho Noria del Verde, 12 April 1932, *Shreve* 5969 (F!); Colonia Miramar, c 3 miles W of Guaymas, 1 July 1974, *Wendt & Chiang* 342 (TEX!); 56 miles N of Hermosillo, 6 May 1948, *Wiggins* 11642 (TEX!); **Sinaloa**, 14 km S of the crossing to La Reforma and Zapotillo on the main route from Los Mochis to Culiacan, 4 March 1990, *Contreras* 2739 (K!); Ejido E Ruiz, 3 km S of border between Sinaloa and Sonora, 4 March 1990, *Contreras* 2732 (K!); Cofradia, 7 Feb. 1940, *Gentry* 5522 (MEXU!, NY!); Isla Tachechilte, 20 Jan. 1945, *Gentry* 7139 (F!, NY!);

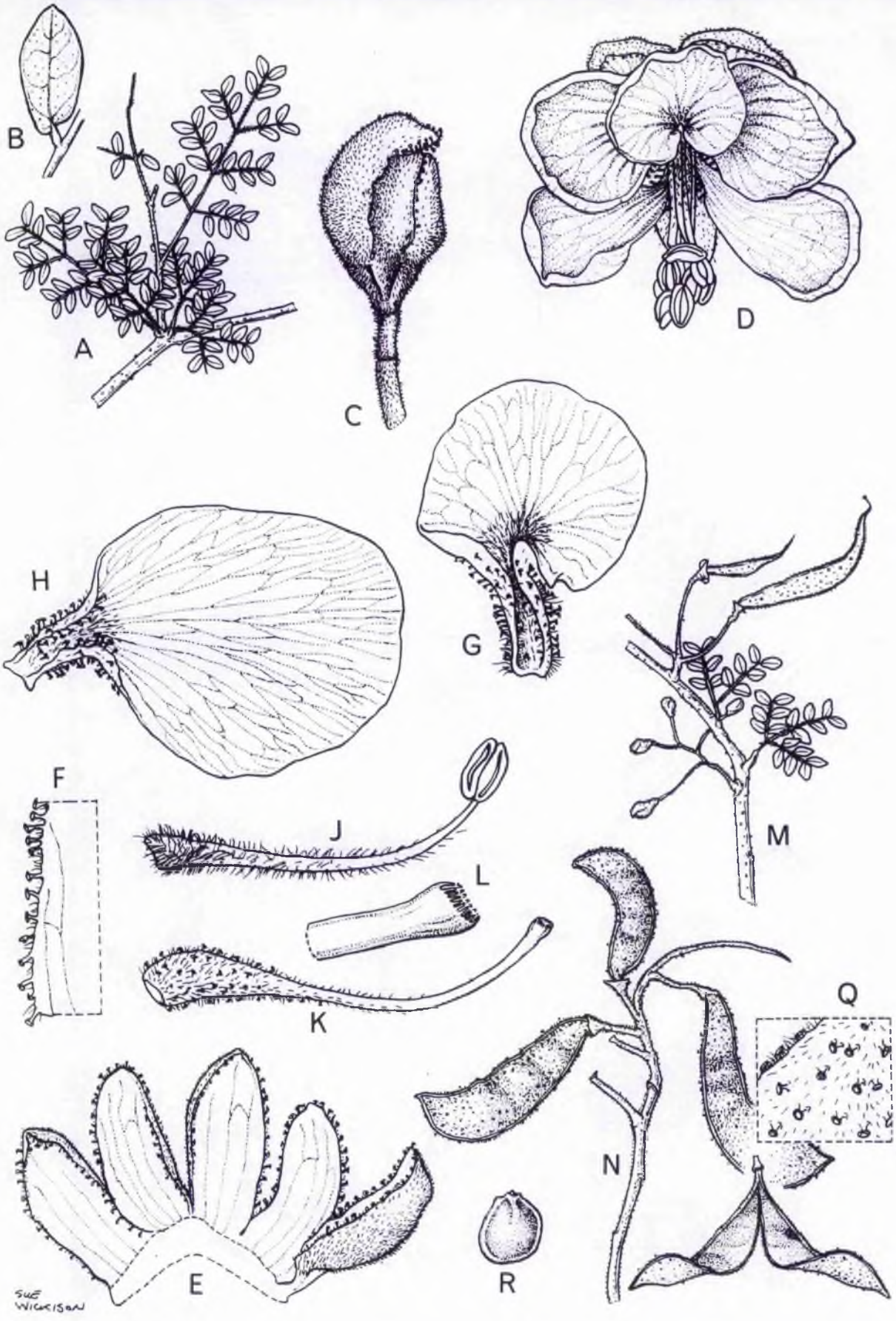


FIG. 22. *Caesalpinia palmeri*. **A** foliage x 1; **B** leaflet undersurface x 4½; **C** bud and pedicel showing articulation zone x 6; **D** flower x 4½; **E** calyx opened out x 6; **F** glandular margin of calyx lobe x 18; **G** standard petal x 9; **H** lateral petal x 9; **J** stamen x 9; **K** gynoecium x 9; **L** stigma x 24; **M** branchlet with developing ovaries x 1; **N** fruits x 1; **P** dehisced fruit x 1; **Q** detail of fruit glands x 6; **R** seed x 1½. **A**, **B** & **N** from *Ortega* 5498, **C** & **M** from *Schreve* 5969, **D** from *Contreras* 2732, **E–L** from *Gentry* 4464, **Q** from *Dillon & Rodriguez* 1041, **P** & **R** from *Palmer* 70. Drawn by Sue Wickison.

38 miles NW of Culiacan, 11 April 1970, *Mahler & Thieret* 5978 (NY!); 28 miles N of Mazatlan, 11 April 1970, *Mahler & Thieret* 5958 (NY!); Mpio. Fuerte, Constancia, without date, *Ortega* 5498 (K!); Mpio. Mazatlan, Bellavista, March 1931, *Ortega* 6830 (F!); Mazatlan, Villa Unión, without date, *Ortega* 188 (MEXU!); near Culiacan, 21 April 1910, *Rose et al.* 14851 (NY!); near Fuerte, 25 March 1910, *Rose* 13486 (NY!); near Mazatlan, 1 April 1910, *Rose et al.* 13871 (NY!); 23 miles S of Guamuchil on highway 15, 26 Dec. 1983, *Sanders et al.* 4248 (NY!); 3 miles N of Sibirijoa on highway 32, 17 March 1983, *Whittemore et al.* 83--036 (TEX!).

ECOLOGY. Tropical deciduous woodland and desert scrub, 20--220 m.

PHENOLOGY. Flowering from November to July, fruiting from December to July.

VERNACULAR NAMES. "Peojo" (Sonora); "Margarita" and "Wetapochi" (Sonora, but cited on Gentry 1378, a mixed collection of *C. palmeri* and *C. caladenia*); "Palo piojo", "Polilla" (Sinoloa).

NOTES. *Mahler & Thieret* 5978 (NY!) is a mixed sheet of flowers and fruits of *C. palmeri* (on the right) and an inflorescence in bud of *C. eriostachys* (on the left). *Gentry* 5222 has small leaves with pubescent rhachides and leaflet blades and, on the same stem, larger, more mature, leaves with all parts glabrous. Leaflets are usually eglandular but on *Ortega* 6830 leaflet margins are glandular. The margins of leaflets are strongly glandular and ± crenulate on *Gentry* 7139 which also has stipitate, pixie-cup glands on the leaf rhachis. Personal observations in Sonora suggest that *C. palmeri* possibly hybridizes with *C. caladenia*. A more detailed account of this is presented under *C. caladenia*. Gentry 1378 from the Rio Mayo, San Bernado is a mixed collection of *C. palmeri* and *C. caladenia*.

10. **Caesalpinia exostemma** *DC.*, Prodr. 2: 483 (1825).

Type: Mexico, a painting, one of the copies of Ic. Fl. Mex. 80, represented at G-DC by deCandolle plate 218.

Unarmed shrub or single to multiple-stemmed tree (2--)4--12 m tall, DBH 8--30 cm, branching contorted, often flowering when leafless; bark greyish, greenish-grey or pale brownish-grey, somewhat shiny, regularly dotted with whitish-cream, pustular lenticels; outer slash pea-green, inner slash whitish-yellow, heartwood brown, slash odour of broad

beans (*Vicia faba*); young stems pubescent with simple hairs and a few stellate or plumose hairs intermixed or with stipitate pixie-cup glands intermixed, the gland stalks hairy, or glabrous. *Leaves* bipinnate; stipules ovate-orbicular, 4 mm long, margin ciliolate, caducous; petiole (2.5--)3.5--7.5 cm long, moderately pubescent to glabrous; rhachis 3--13.5 cm long, densely pubescent to glabrous; pinnae in 2--5 opposite pairs plus a terminal pinna; leaflets in (3--)4--6 opposite pairs, petiolulate, often drying mottled, terminal leaflets elliptic-ovate, 1.6--3.6 x 0.7--1.7 cm, median leaflets elliptic to obovate-elliptic, 1.4--3.5 x 0.7--1.5 cm, apex acute to obtuse,base asymmetric, margin revolute, both surfaces of all leaflets densely pubescent to glabrous, secondary venation brochidodromous, blades eglandular,margin sometimes sparsely and obscurely glandular, gland-tipped appendages at pinnae and petiolule insertions. *Inflorescence* a terminal or lateral, sessile, short compact or long pyramidal raceme to 35 cm long, 40--100-flowered, finely puberulous to densely tomentose, eglandular; bracts ovate, acute, 2.5--4 mm long, densely tomentulose or puberulous, caducous; pedicels 1.3--2.5 cm long, puberulous, occasionally short, peg-like glands scattered amongst indumentum, articulated 3--6 mm below calyx. *Calyx* shrimp-pink or salmon-pink to orangish, the upper and lateral lobes broadly ovate-triangular 6--8 mm long, the apices rounded to obtuse, the margins frayed, outer surface puberulous, lower lobe (7--)8--9 mm long, cucullate. *Flowers* laterally compressed, upper part of calyx gibbous, pedicel excentric; petals yellow, eglandular, the standard with a dark orangish-scarlet central blotch, its blade depressed-orbicular to broadly ovate, longitudinally folded, 9--13 x (6.5--)7--10 mm (including a 3--4 mm claw), claw thickened, the margins pubescent at the base, the apex with a glabrous, thickened ridge (or this lacking); upper lateral petals suborbicular to ovate-elliptic or broadly obovate, (11--)12--16 x 8--14 mm (including a 1--2 mm claw), lower laterals obovate-elliptic to elliptic, (11.5--)14--18 x 6--14 mm (including a 1.5--2 mm claw), all laterals with claws sparsely pubescent at base and sometimes with a few short-stalked glands on claw margins and basal $^1/_3$ of blade margin, blades changing colour from yellow to orange to dark red with age. Stamen filaments whitish-cream near base (mainly due to pubescence), dark pinkish-red on upper $^1/_2$, held downwards, 1.3--2.8 cm long, the longest slightly longer than to about twice the length of the petals, densely pubescent on basal $^1/_5$--$^1/_2$, less so on upper $^1/_2$, anthers dark pinkish-red 1.5--2.5 x 1--1.5 mm. Ovary densely pubescent, eglandular or glandular with sessile and stipitate pixie-cup glands, the gland

stalks hairy, 5--7-ovulate; style c 11--20 mm long; stigma a terminal, tubular (narrower than style) chamber, not fringed or ± fringed but the fringe cells fused. *Pod* subligneous, explosively dehiscent, (6.4--)8.5--12 x 1.7--2.4 cm, sparsely to moderately pubescent or glabrescent, eglandular or glandular with reddish glands, 3--6-seeded, calyx lobes early caducous, hypanthium persists as a ring at fruit base. *Seeds* suborbicular to quadrate, 9--12 x 8--10.5 x 1.5--2 mm, yellow or yellowish-brown, sometimes with vertical reddish streaks, shiny. *Seedling* germination phaneroepigeal, cotyledons foliaceous, apex rounded, base cordate, first eophyll pinnate with 4 pairs of opposite leaflets, second eophyll bipinnate with one pair of opposite pinnae plus a terminl pinna, each with 3 pairs of opposite leaflets, hypocotyl glabrous, epicotyl pubescent and glandular.

10a. subsp. **exostemma**

? *Poinciana compressa* Sessé & Mociño ex G. Don, Gen. Hist. 2: 433 (1832). Type: Mexico, *Sessé & Mociño,* formerly in herb. Lambert - not located in recent times, but a specimen in the Sessé & Mociño herbarium (MA), no. 1097, labelled *Poinciana compressa*, represents *C. exostemma* according to P. Standley (fide McVaugh, 1987).

? *Caesalpinia compressa* (G. Don) D. Dietr., Syn. Pl. 2: 1494 (1840).

Caesalpinia affinis Hemsley, Diag. Pl. Nov. 8 (1878). Type: Guatemala, *Skinner* s.n. (holotype K! isotype K!).

Poinciana conzattii Rose in Contribs. U.S. Nat. Herb. 13: 303 (1911). Type: Mexico, Tehuantepec, 1909, *Hugo & Conzatti* 2444 (holotype US!, national herbarium number 841055).

Poincianella exostemma (DC.) Britton & Rose in N. Amer. Fl. 23(5): 328 (1930).

Poincianella affinis (Hemsley) Britton & Rose, loc. cit.: 328 (1930).

Poincianella conzattii (Rose) Britton & Rose, loc. cit.: 328 (1930).

Caesalpinia conzattii (Rose) Standley in Tropical Woods 37: 34 (1934).

Inflorescence a terminal, compact or long pyramidal raceme, standard petal claw with a thickened, glabrous apical appendage, lateral petal claws and blade bases eglandular, stamen filaments 2.5--2.8 cm long, the longest about twice the petal length, well exserted,

style c 2 cm long, leaflet blade and margin eglandular, pod 8.5--12 x 1.8--2.4 cm, plant (2--)4--12 m tall. (Figs. 2A, 7L, 9B, 13A & B, 23, 24D & E, Map 8).

DISTRIBUTION. Mexico, Guatemala, Honduras, El Salvador, Nicaragua and Costa Rica. Cultivated in Cuba (one record).

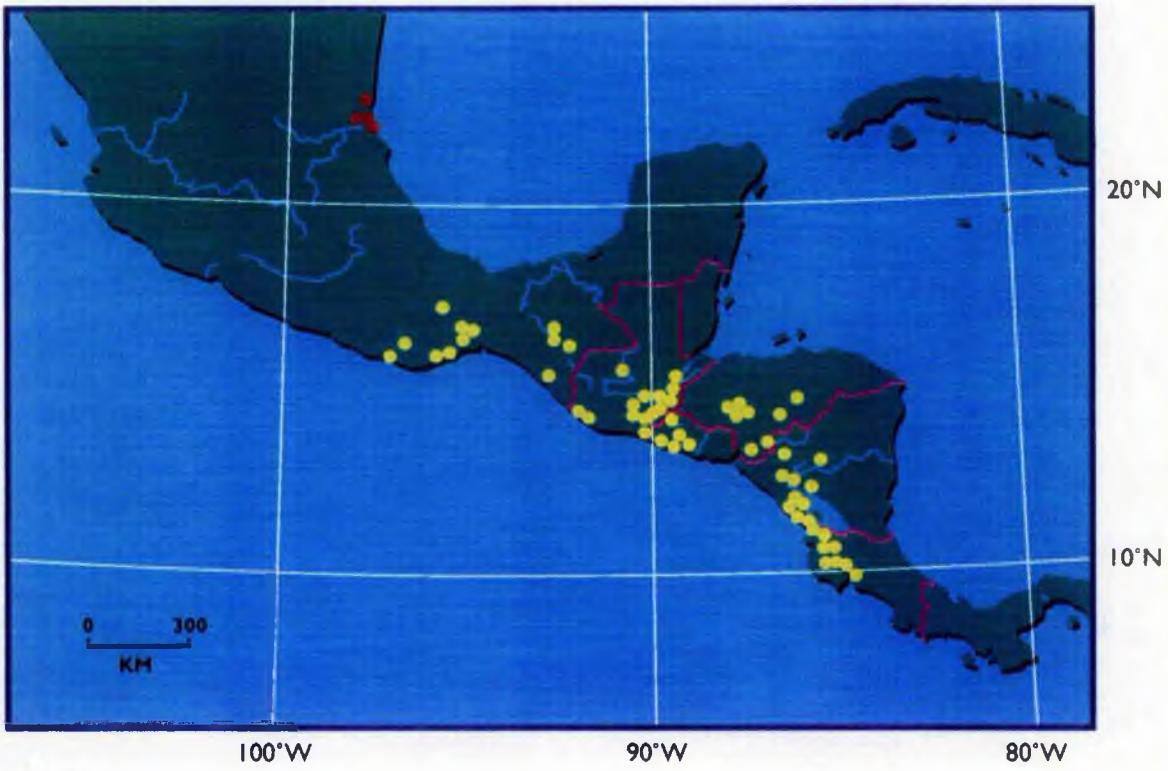
MEXICO: Oaxaca, Tehuantepec, Cerro tigre, 22 Jan. 1945, *Alexander* 2394 (MEXU!, NY!, US!); 42 km SW of Salina Cruz on rd. to Pochutla, 30 Jan. 1992, *Atkinson & MacQueen* 5 (EAP, FHO, K!, MEXU); Oaxaca, garden of Conzatti, 10 March 1949, *Carlson* 1441 (F!); Oaxaca, 24 Feb. 1924, *Conzatti* s.n. (US!); Oaxaca, March 1849, *Galeotti* 3492 (BR!); village of Santiago Laollaga, c 30 km N of Tehuantepec, 11 March 1989, *Lewis & Hughes* 1779 (FHO!, K!, MEXU!, NY!); c 50 km W of Salina Cruz on rd. to Pochutla, 28 March 1989, *Lewis et al.* 1804 (FHO!, K!, MEXU!, NY!); Tehuantepec, Las Tejas, 12 Jan. 1969, *MacDougall* s.n. (NY!); Tehuantepec, 18 Jan. 1951, Mejorada 527 (MEXU!); San Geronimo, 4 April 1930, *Mell* 638 (F!); 18 March 1934, *Mell* 2208 (NY!); La Mistequilla, 14 Jan. 1896, *Seler* 1618 (K!, NY!); Distr. Tehuantepec, Magdalena Tequisixtlán, 19 Feb. 1978, *Sousa et al.* 9091 (MEXU!); Distr. Juchitán, Mpio. Santo Domingo, 2 km NE of La Venta, 21 Feb. 1978, *Sousa et al.* 9151 (MEXU!); 3 km W of Tehuantepec, 14 Dec. 1978, *Sousa et al.* 10092 (MEXU!); 2 km NW of Santiago Laollaga, Distr. Tehuantepec,14 Dec. 1978, *Sousa et al.* 10170 (MEXU!); Hierba Santa, 5 km NW of turning to Guiengola, 17 Feb. 1982, *Torres & Cedillo* 44 (MEXU!); Dist. of Juchitan, La Venta, 13km S of La Ventosa, 24 Feb. 1981, *Trigos* 550 (MEXU!, NY!); **Chiapas**, Mpio. Trinitaria, dirt road to Boqueron, 8 Dec. 1976, *Breedlove* 42280 (MEXU!); Mpio. of Chiapilla, Rio Grijalva, 25 Feb. 1966, *Laughlin* 245 (US!); c 25 km SE of Tuxtla Gutierrez, near Villa de Acala, 9 March 1989, *Lewis & Hughes* 1776 (FHO!, K!, MEXU!, NY!); 11 km N of Mapastepec toward Arriaga, 29 Jan. 1992, *MacQueen & Atkinson* 388 (EAP, FHO, K!, MEXU); **GUATEMALA**, Dept. Quiché, 1942, *Aguilar* 1071 (F!); Gualan, 17 Jan. 1905, *Deam* 293 (MO!, US!); Dept. Chiquimula, near Petapilla, 19 March 1988, *Hughes* 1116 (K!); Dept. El Progresso, San Agustin Acasaguastlán, 8 Jan. 1983, *Hughes* 264 (K!, MEXU!); Progresso, 1 Jan. 1938, *Johnston* 1151 (EAP!, F!); Champerico, 21 Feb. 1941, *Johnston* 1734 (F!); Jalapa, El Rancho, 20 Jan. 1908, *Kellerman* 8014 (F!, NY!); Motagua Valley, c 12 km W of Zacapa, 12 Feb. 1989, *Lewis & Hughes* 1712 (FHO!, K!, MEXU!); c 10 km E of El Rancho on rd. from El Progresso to Zacapa, 27 Feb. 1989, *Lewis & Hughes* 1753 (FHO!, K!, MEXU!, NY!); *Lewis & Hughes* 1752 (FHO!, K!, MEXU!); c 20--25 km W of Jutiapa on highway CA 1 to Guatemala City, 26 Feb. 1989, *Lewis & Hughes* 1751 (FHO!, K!, MEXU!, NY!); Dept. Santa Rosa, 1 km N of Casillas on rd. to Laguna Ayarzo, 25 Jan. 1992, *MacQueen* 373 (EAP, FHO, K!, MEXU); Dept. El Progresso, 8 km from Sanarate on rd. to El Progresso, 16 Feb. 1991, *MacQueen* 58 (EAP, FHO, K!, MEXU, MO); Dept. Santa Rosa, c 30 km from Chiquimulilla towards El Obraje on Salvadorean border, 15 Feb. 1991, *MacQueen* 54 (EAP, FHO, K!, MEXU, MO); near Zacapa, Jan. 1907, *Pittier* 1766 (NY!); Zacapa, dirt road W of La Fragua, 5 Dec. 1977, *Ramos & Funk* 523 (MEXU!); Baranquillo, April 1932, *Sálas* 1461 (F!); without locality or date, *Skinner* s.n. (?27) (K!); Dept. Guatemala,

FIG. 23. *Caesalpinia exostemma* subsp. *exostemma*. **A** bipinnate leaf x 1; **B** median leaflet undersurface x 1½; **C** bark section x 1½; **D** inflorescence in bud x 1; **E** young inflorescence apex showing bracts x 1; **F** inflorescence x 1; **G** calyx opened out x 3; **H** standard petal x 4½; **J** detail of standard claw x 6; **K** upper lateral petal x 4½; **L** stamen x 4½; **M** gynoecium x 4½; **N** stigma x 15; **P** glandular fruit x 1; **Q** detail of fruit glands x 6; **R** eglandular fruit x 1; **S** & **T** patterned and unpatterned seeds x 1½; **U** seedling x 1; **V** flower visitor – carpenter bee x 1½. **A**, **B** & **E** from *Lewis & Hughes* 1709, **D** from *Lewis & Hughes* 1717, **F** from *Lewis & Hughes* 1751, **C** & **G–N** from *Lewis & Hughes* 1708, **P–T** from *Lewis & Hughes* 1712. Drawn by Sue Wickison.

FIG. 24. *Caesalpinia coccinea*: **A** flowers (*Lewis et al.* 1802, type); *C. hughesii*: **B** long racemose and short paniculate inflorescences (*MacQueen et al.* 409); **C** inflorescence (*MacQueen et al.* 409); *C. exostemma* subsp. *exostemma*: **D** flower, cultivated Kew (*Lewis & Hughes* 1712); **E** inflorescence (*Lewis & Hughes* 1709).

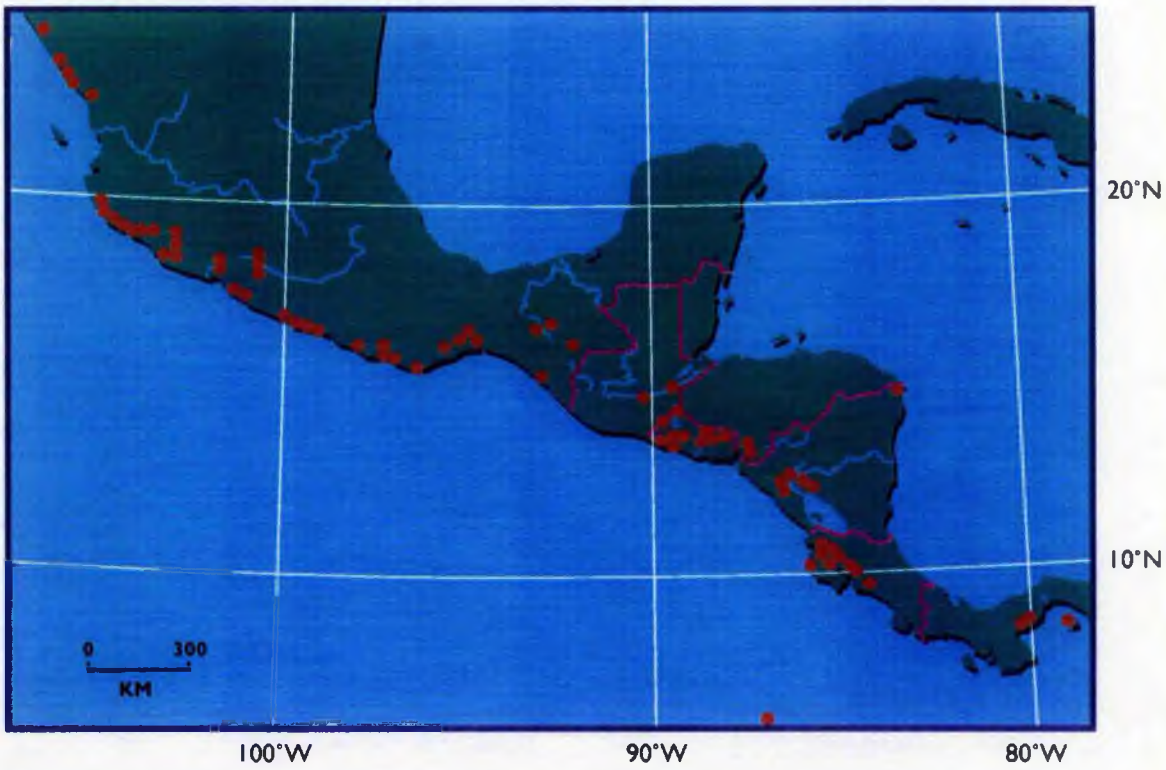
Map 8

Distribution of *Caesalpinia exostemma* subsp. *exostemma* (○) and *C. exostemma* subsp. *tampicoana* (●) in Mexico and Central America



Map 9

Distribution of *Caesalpinia eriostachys* (●) in Mexico and Central America



Feb. 1890, *Smith* 2294 (K!); Amatitlan, May 1892, *Smith* 2828 (K!); Dept. Zacapa, Baños de Santa Marta, 10 Oct. 1940, *Standley* 73933 (F!); Dept. Chiquimula, nr. divide of rd Chiquimula to Zacapa, 22 April 1939, *Standley* 71960 (F!); *Standley* 71963 (F!); *Standley* 71974 (F!); Dept. Retalhuleu, between Nueva Linda and Champerico,18 Feb. 1941, *Standley* 87524 (F!); *Standley* 87687 (F!); 25 Feb. 1941, *Standley* 88419 (F!); Dept. Zacapa, between Teculután and Monte Grande, 8 Jan. 1942, *Steyermark* 42174 (F!), Dept. El Progresso, between Tulumajillo and Finca Montañita, 3 Feb. 1942, *Steyermark* 43341 (F!); Dept. Sta. Cruz, 6 km NW of Barberena, El Serenal, 12 April 1978, *Tellez et al.* 620 (MEXU!); without locality or date, *Wendland* s.n. (K!); **HONDURAS**, Comayagua, 20 Feb. 1933, *Edwards* 565 (A!, F!, K!); 20 km NE of Choluteca, 17 March 1982, *Hughes & Styles* 97 (K!, NY!); 8 km SW of Comayagua on rd. to El Taladro, 10 Feb. 1989, *Lewis & Hughes* 1708 (EAP!, F!, FHO!, K!, MEXU!); Los Cascabeles, c 3 km S of El Taladro, 10 Feb. 1989, *Lewis & Hughes* 1709 (EAP!, FHO!, K!, MEXU!); Dept. Olancho, rd. to San Francisco de La Paz, 20 Nov. 1963, *Molina* 13341 (EAP!, F!, NY!); Dept. El Paraiso, nr. Oropoli, Rio Choluteca, 9 March 1958, *Molina* 8618 (EAP!, F!, US!); Dept. Comayagua, El Borneo, 14 March 1945, *Rodriguez* 2376 (F!); Dept. Comayagua, between Comayagua and Villa de San Antonio de Flores, 1 May 1947, *Williams & Molina* 12596 (EAP!, F!, MEXU!); **EL SALVADOR**, W of La Libertad on coastal highway, 28 Jan. 1959, *Allen* 7200 (EAP!, F!, GH!, LL!, NY!); San Salvador, May 1922, *Calderón* 736 (NY!); Santa Tecla, Feb. 1923, *Calderón* 1497 (NY!); Finca Santa Emilia W of La Libertad, 11 Feb. 1946, *Carlson* 561 (F!); without locality or date, *Kovar* 1089 (F!); Dept. Santa Ana, c 3 km S of San Geronimo on rd. to Metapan, 22 Feb. 1989, *Lewis et al.* 1746 (FHO!, K!, LAGU!, MEXU!); San Salvador, Jardin Botânico La Laguna, 15 Feb. 1989, *Lewis & Hughes* 1717 (FHO!, K!, LAGU!, MEXU!); c 18--20 km W of Acajutla on highway CA 2, 16 Feb. 1989, *Lewis et al.* 1720 (FHO!, K!, LAGU!, MEXU!); near San Salvador, without date, *Renson* 114 (NY!); Dept. San Salvador, near Ayutuxtepeque, 3 Feb. 1922, *Standley* 20526 (NY!); Dept. of Sonsonate, nr. Acajutla, 20 March 1922, *Standley* 21981 (NY!); Dept. Ahuachapán, 16--25 Jan. 1947, *Standley & Padilla* 2785 (EAP!, F!); **NICARAGUA**, Dept. of Rivas, 18 km S of San Juan del Sur, 10 Feb. 1980, *Araquistain & Moreno* 1221 (MEXU!); Dept. of Leon, Volcán Momotombo, 29 Jan. 1980, *Araquistain & Moreno* 1098 (MEXU!); Dept. Metagalpa, nr. Dario, 3 March 1961, *Bunting & Licht* 370 (F!, NY!, US!); Santa Maria de Ostuma, 1960--61, *Heller* 11 (F!); Dept. of Esteli, 10 km NE of San Juan de Limay, 19 Feb. 1982, *Hughes & Styles* 36 (K!, MEXU!); Dept. Boaco, 10 km from Tecolosote on highway 7 to Boaco, 17 Jan. 1991, *MacQueen et al.* 5 (FHO, K!); Dept. Rivas, 10 km from Rivas to Penas Blancas, 1 April 1991, *MacQueen* 97 (EAP, FHO, K!, MEXU, MO); Granada,1845--1848, *Oersted* 5068 (F!); *Oersted* 5055 (F!); *Oersted* 5060 (F!); Dept. Zelaya, nr. El Recreo, 23 April - 14 May 1949, *Standley* 19606 (EAP!, F!); Dept. Rivas, SE of San Juan del Sur, Rio Escameca Grande,17 Dec. 1977, *Stevens* 5512 (MEXU!, NY!); Dept. Managua, 1.5--3.5 km N of Las Maderas, 26 Dec. 1978, *Stevens* 11286 (MEXU!); Dept. Esteli, La Grecia, 23 Jan. 1981, *Stevens* 18993 (NY!); Dept. Carazo, between Amayito and Barranco Bayo, 12 Jan. 1984, *Stevens* 22732 (LSU!); Dept. Metagalpa, 5--10 km W of Metagalpa, 13 Jan. 1963, *Williams et al.* 23759 (F!); **COSTA RICA**, Guanacaste Province,Parque Nacional of Santa Rosa, 27 Feb. 1978, *Almeda & Nakai* 3979 (MEXU!); Prov. Guanacaste, W of La Cruz, nr. E side of Bahia de Salinas, 12 May 1968, *Burger & Stolze* 4860 (F!, NY!); 1 km NW of Colorado, 14 Jan. 1969, *Davidse & Pohl* 1432

(LL!, MO!); Guanacaste, NW of Paloverde, Barbudal Hills, 26 Jan. 1983, *Garwood et al.* 603 (F!); E shore of Nicoya Peninsula, 3 km N of El Roblar,5 April 1986, *Hughes* 803 (K!); between Comunidad and Filadelfia, 20 March 1963, *Jimenez* 486 (EAP!, F!); Puntarenas, 5 Nov. 1941, *Léon* 496 (F!); Santa Rosa National Park, 21 Jan. 1978, *Liesner* 4292 (MO!); 5 km W of Santa Cruz, 29 Jan. 1973, *Opler* 1681 (F!); Puntarenas, Boca de la Barranca, 2 March 1940, *Quiróz* 937 (F!); Guanacaste, 3 km E of Cuajinicuil, 26 Jan. 1983, *Sousa et al.* 12718 (MEXU!); **CUBA**, cultivated, Est. Exp. Agronomica, Prov. Habana, Oct. 1940, *Roig* 10738 (HAC!).

ECOLOGY. Deciduous tropical forest, open dry thorn shrub, frequently cultivated as a garden ornamental or in living fence-lines, 1--750(--1500) m.

PHENOLOGY. Flowering from November to May, fruiting from December to June.

VERNACULAR NAMES. "Abejon", "Quete Regal", "Yagati" (Mexico), "Carcomo", "Ebano", "Gallito" (Guatemala), "Guacamaya" (Honduras), "Camaroncillo", "Carbón", "Flor del Mar", "Flor mareña", "Gallito" (El Salvador), "Palo de manteca" (Nicaragua).

NOTES. My findings concur with those of Contreras (1991) in recognising *C. affinis* and *C. conzattii* as synonyms of *C. exostemma*. *C. compressa* (G. Don) Dietr. is also placed in synonymy here following McVaugh (1987). *C. exostemma* subsp. *exostemma* is a widely distributed taxon displaying a high degree of character variation, especially as to indumentum of foliage, fruits and inflorescences, presence or absence of glands on various organs, size of flowers and form of inflorescence. Within a population, individual trees can have all fruits eglandular or all densely glandular. Higher altitude specimens tend to have smaller flowers and often hairier leaflets (e.g. *Edwards* 565, a 12 metre tree from c 600 m in Honduras and *Heller* 11, from 1200--1500 in Nicaragua). Specimens from coastal Costa Rica and El Salvador tend to have larger flowers, inflorescences and fruits and the calyces usually dry a dusky pink. Robber bees frequently chew through the calyx tube to steal nectar but humming birds and solitary carpenter bees seem to be the main pollinators. A detailed study of the pollination of this and related species would make a fascinating field project.

10b. subsp. **tampicoana** *(Britton & Rose)* G.P. Lewis, stat. & comb. nov., in sched.

Poincianella tampicoana Britton & Rose in N. Amer. Fl. 23(5): 330 (1930).

Type: Mexico, Vera Cruz, vicinity of Pueblo Viejo, 2 km S of Tampico, 1--2 . June 1910, *Palmer* 556 (holotype US!).

Caesalpinia tampicoana (Britton & Rose) Standley in Publ. Field Mus. Nat.

Hist. Chicago, Bot. Series 11(5): 159 (1936).

Inflorescence a compact ramiflorous terminal or lateral raceme, standard petal claw lacking apical appendage, lateral petals with short-stalked glands on claw margin and lower $^1/_3$ of blade margin, stamen filaments 13--16 mm long, only slightly longer than the lower lateral petals, style 11--12 mm long, leaflet blade eglandular, the revolute margin sparsely glandular, pod 6.4--6.7 x 1.7--1.8 cm, plant 2--3 m tall. (Map 8).

DISTRIBUTION. Mexico in the states of Veracruz and Tamaulipas.

MEXICO: Tamaulipas, Moron, 3 Aug. 1939, *Le Sueur* 188 (F!); 2 mi. NE of Altamira, 3 March 1961, *King* 4015 (F!, US!); **Veracruz**, 3 km E of Tamaulipas - Veracruz state line, 7 km SE of Ebano [estado San Luis Potosí], Mun. Pánuco, 7 March 1983, *Nee & Taylor* 25792 (F!, K!); 2 km S of Tampico, nr. Pueblo Viejo, 1--2 June 1910, *Palmer* 556 (holotype US!).

ECOLOGY. Low shrub oak forest, grazed thorn scrub in low deciduous woodland, 55 m.

PHENOLOGY. Known to flower in March, June and August, the only fruiting material examined in this study was collected in June.

NOTES. A little-known east Mexican taxon of *C. exostemma* which differs from the typical variety principally by its smaller flowers and fruits, stamens little exserted and lack of standard claw appendage. The holotype, *Palmer* 556 at US, bears two branchlets, one with the leaflets essentially glabrous, the other with the leaflets pubescent on both surfaces.

11. **Caesalpinia hughesii** *G.P. Lewis* sp. nov. in sched.

Type: Mexico, Oaxaca, 5 km W of Rio Grande, 25 March 1989, *Lewis et al.* 1795 (holotype K!, isotypes FCME!, FHO!, K!, MEXU!).

Unarmed, multiple-trunked tree (occasionally coppiced and shrub-like), 2--10 m tall, trunk up to 30 cm in diam., main branches 10--15 cm in diam.; bark greyish-green or

brownish-green with numerous white, pustular lenticels, outer bark slash pea-green with a smell of broad beans (*Vicia faba*), inner slash cream or peach coloured; stems essentially glabrous. *Leaves* bipinnate; petiole 3--5.7 cm long, glabrous, very sparsely pubescent at base or totally pubescent; rhachis 9.2--14.5 cm long, glabrous or pubescent; pinnae in 3--5 opposite pairs plus a terminal pinna (rarely ending in a pair); leaflets in 4--7 opposite pairs, petiolulate, oblong-elliptic, apex rounded or obtuse, mucronulate, base inequilateral, margin strongly revolute, terminal leaflets 3--3.2(--4) x 1.2(--2) cm, medians 2.3--2.8(--3.3) x 0.9--1.1(--1.7) cm, upper surface very sparsely pubescent to glabrous, lower surface pubescent (sometimes only on the prominent main vein and petiolule) to glabrous, secondary venation brochidodromous, blades eglandular. *Inflorescence* a lateral or terminal, 30--multi-flowered short or long raceme, up to 40 cm long, or a little-branched terminal panicle, the rhachis and pedicels puberulous; bracts ovate, acute, 3--3.5 mm long, caducous; pedicels 13--20(--24) mm long, articulated 5--7 mm below calyx. *Calyx* tube yellow, tinged green near base, upper and lateral lobes broadly ovate-triangular, obtuse, 7--11 mm long, puberulous, lower lobe broadly ovate, concave, 9--12 mm long, the apex frayed, the lobes often persisting to fairly mature fruit. *Corolla* yellow, laterally compressed; standard petal with a central scarlet-orange blotch, the blade compressed-ovate, obtuse, 13--15 x 6--12 mm (including a 4 mm claw), eglandular, the claw thickened, pubescent at base, sparsely so on grooved inner surface, the apex with two thickened, pubescent appendages or a pubescent dentate ridge; upper lateral petals suborbicular to broadly obovate, 15--17 x 10.5--16 mm (including a 3 mm claw), claw sparsely pubescent on margin at base and very sparsely so on inner surface; lower laterals obovate-elliptic to ovate-elliptic or spathulate, 17--20 x 9--11.5 mm (including a 4--5 mm claw), claw very sparsely pubescent on margin at base, all lateral petals with claws relatively wide, the margins stipitate-glandular with long-stalked pixie-cup glands, sometimes densely glandular and with additional glandular flanges, outer surface of claw with a few stipitate glands. Stamen filaments greenish, 2--2.4 cm long, relatively thick and rigid, wider at base than apex, densely pubescent on basal ¼ (with hairs interwoven so that stamens are difficult to separate from each other) some filaments in each flower densely pubescent to their apices (especially on their inner surfaces); anthers yellow, 2 x 1 mm. Ovary densely pubescent, eglandular or moderately stipitate-glandular, 5--6(--?9)-ovulate; style c 17 mm long, thickened towards apex, moderately pubescent on basal ½;

stigma a terminal, tubular, fringed chamber (the fringe cells fused). *Pod* woody, explosively dehiscent, 11--12 x 2.2 cm, puberulous or tomentulose, eglandular, 5--6(--?8-seeded. *Seeds* yellow-ochre, usually with vertical red bands or streaks, suborbicular, broadly ovate, ovate-elliptic to subquadrate, 11.5--12.5 x 10.5--11.5 x 2--2.5 mm. *Seedling* germination phaneroepigeal, cotyledons foliaceous, apex rounded, base cordate, first eophyll pinnate with 5 pairs of opposite leaflets, second eophyll alternate to first, bipinnate with one pair of opposite pinnae plus a terminal pinna, each with 2--4 pairs of opposite leaflets. (Figs. 1A & B, 10A, 13C, 24B & C & **25**, Map 10).

DISTRIBUTION. Mexico in the states of Colima, Michoacan, Guerrero and Oaxaca.

MEXICO: Colima, Mpio. Manzanillo, near Manzanillo, 9 March 1981, *Magallanes* 2832 (MEXU!); **Michoacan**, Nasco,Feb. 1899, *Langlassé* 823 (K!); **Guerrero**, W of Acapulco on Hwy 200, 4 Feb. 1971, *Freeland & Spetzman* 145 (MEXU!); 19 km W of San Marcos on road to Acapulco, 7 Feb. 1992, *MacQueen* 409 (K!); **Oaxaca**, Santa Rosa, between Mitla and Puerto Escondido, 18--22 Feb. 1966, *Ernst* 2820 (MEXU!); Mpio. el Espinal, c 60 mi. WNW of Puerto Angel on highway 200 to Acapulco, 13 March 1985, *Grimes et al.* 2637 (NY!); 1 km inland from Bahias de Santa Cruz, 40 km E of Pochutla, 9 Feb. 1987, *Hughes* 839 (K!); 4 km N of El Coyol on rd. to Pochutla, 30 Jan. 1992, *MacQueen & Atkinson* 391 (EAP, FHO, K!, MEXU); rd. Rio Grande to Santiago Jocotepec, 4 km N of main highway between Pinotepa Nacional and Puerto Escondido, 26 Nov. 1991, *MacQueen* 270 (EAP, FHO, K!, MEXU); 5 km W of Rio Grande on highway to Pinotepa Nacional, 25 March 1989, *Lewis et al.* 1795 (holotype K!, isotypes FCME!, FHO!, K!, MEXU!); Mpio. Cozoaltepec, San Juanito to Cozoaltepec, 27 Feb. 1974, *Sousa et al.* 4376 (MEXU!); Cacalote, 7 km SE of Rio Grande, 40 km NW of Puerto Escondido, 19 April 1976, *Sousa et al.* 5550 (MEXU!, MO!); Agua Zarca, 6 km E of Rio Grande, distr. Juquila, road from Jamiltepec to Puerto Escondido, 5 Feb. 1977, *Sousa et al.* 7081 (MEXU!); Distr. Pochutla, 2 km N of Barra de Sta. Elena, 6 Feb. 1977, *Sousa et al.* 7110 (MEXU!); Distr. Pochutla, 6 km W of Pochutla, 9 Feb. 1977, *Sousa et al.* 7152 (MEXU!); Distr. Juquila, 3.2 km N of Puerto Escondido on road to Oaxaca, 13 Feb. 1983,*Torres et al.* 2263 (MEXU!).

ECOLOGY. Tropical deciduous forest and roadside scrub, 15--130 m.

PHENOLOGY. Flowering and fruiting January to March.

VERNACULAR NAME. "Quebrache".

NOTES. This new species is closely related to *C. exostemma* and appears very similar as pressed herbarium material. It is, however, separable by a consistently different suite of characters: the peduncle and inflorescence rhachis are more robust and longer, the

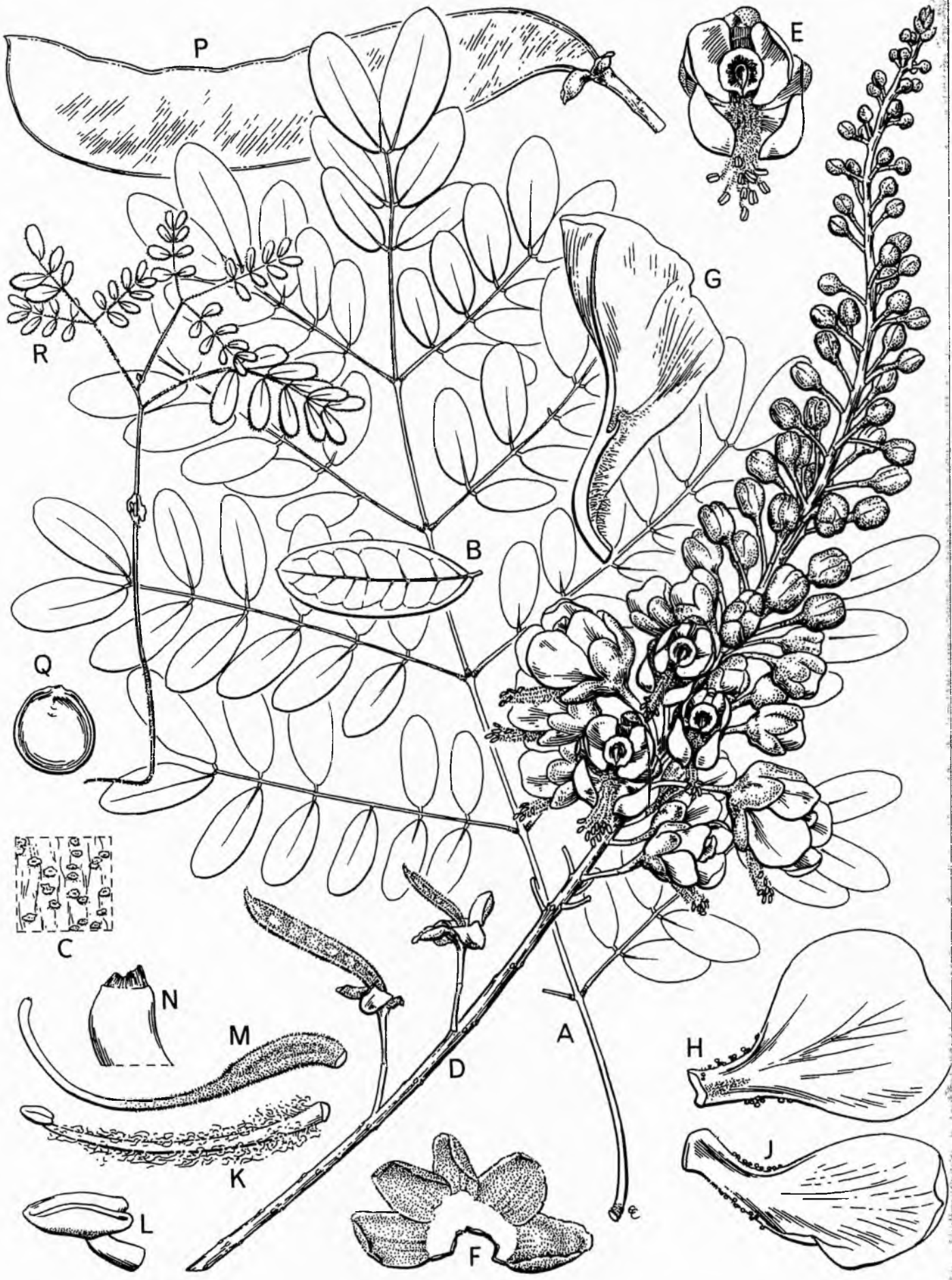
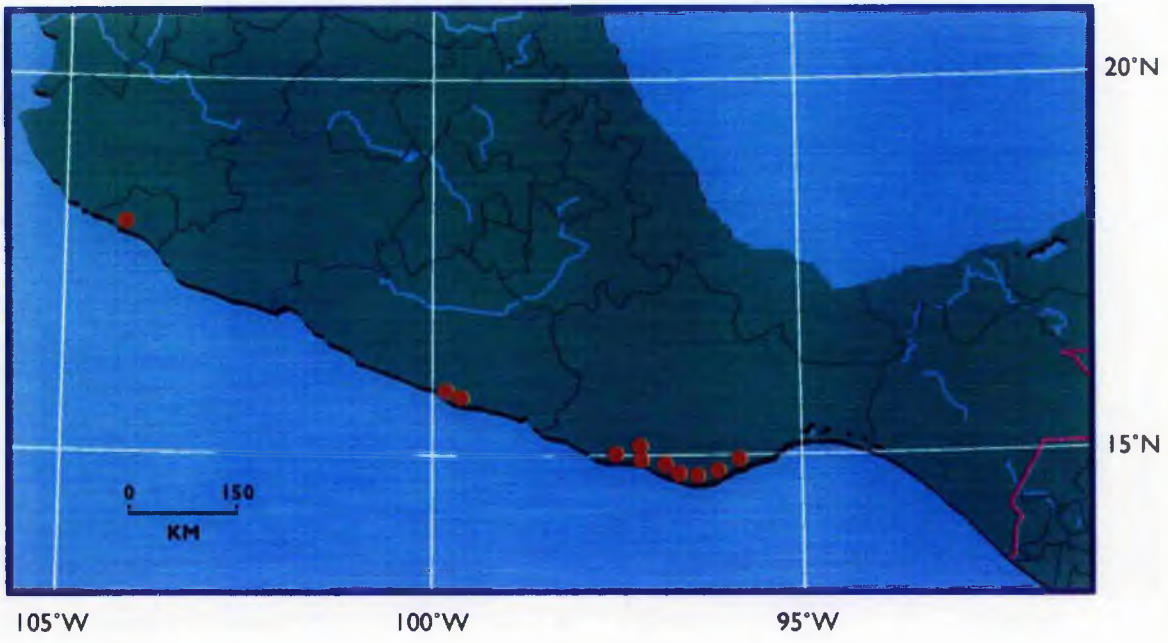


FIG. 25. *Caesalpinia hughesii*. **A** bipinnate leaf x 1; **B** leaflet undersurface x 1½; **C** section of bark x 1; **D** inflorescence x 1; **E** flower front view x 1½; **F** calyx opened out x 1½; **G** l.s. of standard petal x 4½; **H** upper lateral petal x 3; **J** lower lateral petal x 3; **K** stamen x 3; **L** anther x 9; **M** gynoecium x 3; **N** stigma x 22½; **P** fruit x 1; **Q** seed x 1½; **R** seedling x ½. All from *Lewis et al.* 1795. Drawn by Eleanor Catherine.

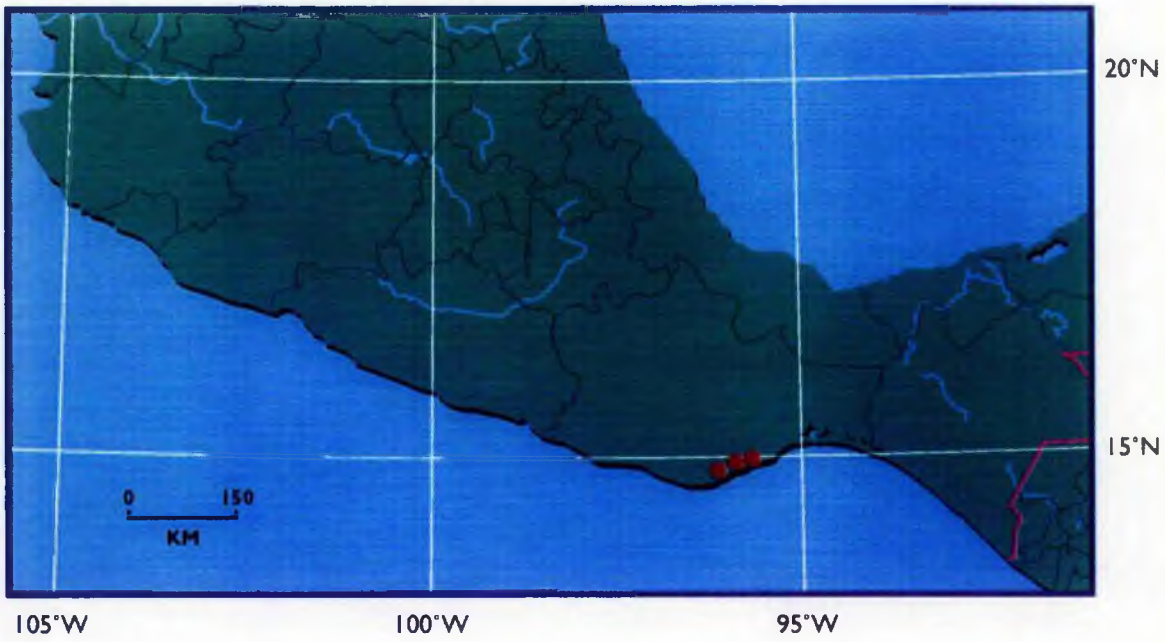
Map 10

Distribution of *Caesalpinia hughesii* (●) in Mexico



Map 11

Distribution of *Caesalpinia coccinea* (●) in Mexico



flowers have relatively shorter stamens that are but a little longer than the petals, the stamen filaments are greenish (not pinkish-red) and are generally densely pubescent for their entire length, the pedicels are articulated 5--7 mm below the calyces, the standard petal is larger, compressed-ovate and its claw has a pubescent (sometimes dentate) ridge at its apex, the lower lateral petals are proportionately longer and narrower and all four lateral petals have claws with stipitate-glandular margins, the calyx lobes are larger and often persist to fruit, and the leaflets have a more pronounced revolute margin.

Bees and humming birds are known to visit the species for nectar. *Lewis et al.* (number 1795) report a small red-beaked humming bird visiting the flowers at 1600 hrs; in reaching the nectar the birds beak splits the standard petal in two. *Sousa et al.* (7152) report that biting ants live in the hollow stems of young branchlets and inflorescence rhachides. Both *Hughes* (839) and *MacQueen* (270) report that the tree is locally frequent but not noted widely. This contrasts with the much more widespread distribution of *C. exostemma*.

12. **Caesalpinia coccinea** G.P. Lewis & J.L. Contr. in Kew Bull. 49: 103 (1994). Type: Mexico, Oaxaca State, 27 March 1989, *Lewis et al.* 1802 (holotype MEXU!, isotypes FCME!, FHO!, K!, M!, NY!, SI!).

Small to medium-sized, single or multiple-trunked shrub or tree 3--10 m tall, DBH up to 20 cm; trunk and main branches crooked, branches knobbly and warted, crown open with a 5--6 m spread; bark greyish-white with a dark green underbark, ornamented with scattered vertical rows of slightly pustular small white lenticels, bark slash creamish. Foliage sparse; *leaves* bipinnate; stipules caducous; petiole up to 5 cm long, glabrous, sometimes with small sessile or short-stalked glands near its base; pinnae in (1--)3--5 pairs plus a terminal pinna; leaflets in (2--)3--4(--5) opposite pairs per pinna, subsessile, ± fleshy, bluish green with purplish-black punctate glands along the margin, elliptic to suborbicular, apex and base rounded, 1.4--1.7(--2.3) x 0.5--1(--1.5) cm, glabrous, the midvein evident only on the lower surface, secondary venation, where evident, brochidodromous. *Inflorescence* a pyramidal raceme (on some branches forming a less showy congested panicle), glabrous; bracts ovate, obtuse, c. 5--6 mm long, glabrous,

early-caducous; pedicels up to 2.3 cm long, articulated 4 mm below calyx base, glabrous, expanding in fruit to 2.7 cm and thickening. *Calyx* glossy lime green, glabrous, 1.3 cm long just prior to anthesis, the lobes 9 mm long, yellow, reflexing when the flower opens, lobe margins ragged due to irregular tearing. *Corolla* dark pinkish scarlet, the glandular claws margined greenish yellow; standard blade c. 10 x 12 mm, the margin glandular, the base inrolled and thickened, claw c.7 mm long, thickened, the inner surface pubescent near the base, margin sparsely glandular; upper lateral petals 1.3 x 1.6 cm (excluding claw), apex emarginate, margin glandular, claw c.6 mm long, thickened and inrolled especially near apex, base with a small tuft of lanate hairs on inner surface, margin with a few stalked glands; lower lateral petals 1.5 x 1.3 cm, apex deeply emarginate, claw c.5 mm long, less inrolled than on upper laterals and lacking tuft of hair at base. Stamens well exserted from petals, 3.5 cm long, filaments yellowish green, white-lanate, densely so at base, sparsely so at apex; anthers 1.75--2 x 1--2.25 mm. Ovary finely tomentose; style pubescent near base, glabrous near apex; stigma terminal, crateriform, fringed by a ring of cells forming a circular pollen-comb. *Fruit* an explosively dehiscent pod, the valves twisting, drying a straw-yellow colour, 9--12 x 2--2.2 cm (including a 3 mm terminal apiculum), tomentose, the hairs most obvious along the sutures, valves with oblique streaks, calyx tube persisting but lobes abscising, up to 7-seeded. *Seeds* yellow (some with a few obscure reddish markings), glossy, c.1 x 1 cm. *Seedlings* phaneroepigeal, foliar cotyledons cordate at base, first eophyll pinnate with 4 pairs of opposite leaflets, second eophyll alternate to first, bipinnate, with one pair of opposite pinnae and a terminal pinna, each with 3 pairs of opposite leaflets. (Figs. 10C, 24A & **26**, Map 11).

DISTRIBUTION. Mexico in the state of Oaxaca.

MEXICO. Oaxaca: 10 km W of Rio Ayuta on main road from Salina Cruz to Pochutla, c. 100 km W of Salina Cruz, 95°55'W, 15°50'N, 7 April 1987, *Hughes* 954 (FHO!, K!, MEXU!); c.10 km E of Coyula off main coastal highway from Pochutla to Salina Cruz, 96°07'W, 15°47'N, 27 March 1989, *Lewis et al.* 1802 (holotype MEXU!, isotypes FCME!, FHO!, K!, M!, NY!, SI!); c. 30 km E of Bahia Santa Cruz on highway 200 to Salina Cruz, 288 km E of Pinotepa Nacional, 95°48'W, 15°55'N, 28 March 1989, *Lewis et al.* 1803 (FCME!, FHO!, K!, MEXU!); Rincon Bamba, 14 km W of Salina Cruz, on main road from Pochutla to Salina Cruz, 15 Dec. 1978, *Sousa* 10144 (MEXU!); same locality, 13 Dec. 1983, *Torres et al.* 4339 (MEXU!); Puerto Angel, 29 Dec. 1953, *MacDougal* s.n. (MEXU!); Puerto Angel, 28 March 1963, *Bravo et*

FIG. 26. *Caesalpinia coccinea*. **A** inflorescence and fruits x 1; **B** part bipinnate foliage x 1; **C** leaflet undersurface x 3; **D** section of bark x 1; **E** flower x 3; **F** flower l.s. x 3; **G** standard petal x 3; **H** upper lateral petal x 3; **J** lower lateral petal x 3; **K** stamen x 3; **L** gynoecium x 3;**M** dehisced fruit x 1; **N** seed x 3. **B** from *Lewis et al.* 1803, the rest from *Lewis et al.* 1802. Drawn by Sue Wickison.

al. 101 (MEXU!); Puerto Angel, 8 Feb. 1966, *Ernest* 2502 (MEXU!, US); Puerto Angel, 8 Feb. 1966, *Delgadillo* 234 (MEXU!).

ECOLOGY. Decidious tropical forest on coast and on dry hills 5 km inland, 0--100 m.

PHENOLOGY. Flowering and fruiting December to April.

NOTES. The species is possibly under threat of extinction due to the rapidly expanding tourist industry which is developing along the coast of Oaxaca and neighbouring Guerrero. It is related to the widespread *Caesalpinia exostemma* but differs by its striking red flowers which are not laterally compressed and have glandular petal margins. The leaflet margins are glandular-punctate, an additional character that distinguishes the species from *C. exostemma*. Humming birds have been observed visiting the flowers of *C. coccinea* but the effective pollinator is, as yet, unknown.

13. **Caesalpinia yucatanensis** *Greenman* in Field Mus. Publ. Bot. 2: 252 (1907). Type: Mexico, Yucatan, near Izamal, 1895, *Gaumer* 371 (holotype F!, isotypes K!, NY!).

Unarmed shrub to single or multiple-stemmed tree, (2--)4--20 m tall, DBH of main stems 5--35 cm, crown variable, either a narrow inverted cone shape or rounded and compact or open with crooked branching; bark of main stems brown with white lenticels, vertically fissured with the outer papery bark splitting to reveal a green underbark, young branchlets whitish-grey with dense, white, pustular lenticels, furrowed, white pubescent with some stellate hairs intermixed, glabrescent, outer bark slash green, inner slash creamish-white. *Leaves* bipinnate; petiole (1.8--)3.5--6(--7.2) cm long, laterally grooved, sparsely pubescent, glabrescent; rhachis (1.8--)4--15 cm long, laterally grooved, sparsely to densely pubescent, glabrescent; pinnae in 2--4 opposite pairs plus a terminal pinna; leaflets in 2--5 opposite pairs per pinna, petiolulate, the petiolule c. 1 mm long, slightly discolorous, darker above, terminal leaflets oblong-elliptic, narrowly elliptic or ovate, apex acute to obtuse or emarginate, (2.5--)3.5--5.3 x (0.8--)1.2--2.1 cm, median leaflets lanceolate-ovate to oblanceolate or elliptic, apex acute, obtuse or emarginate (1--)2.3--4.7 x (0.4--)0.9--2.4 cm, both surfaces of all leaflets pubescent to glabrous, the upper surface

sometimes shiny; main vein prominent below, secondary venation brochidodromous, tertiary venation obscure; leaflets eglandular or, rarely, with a few dark punctate or subepidermal glands on the revolute margin of the leaflet blade base. *Inflorescence* an axillary or terminal, lax, pyrammidal or compact, chubby raceme to many-branched panicle, each raceme with (25--)50--70 flowers, the rhachides and pedicels sparsely to moderately pubescent, sometimes with a few sessile or short-stalked mushroom-shaped glands intermixed, or glabrous; bracts ovate-lanceolate, acute to acuminate, 4--5.5 x 2--2.5 mm, recurved at the apices, puberulous; pedicels 1--2.8 cm long, articulated (3--)5--7 mm below hypanthium. *Calyx* tube 3--4 mm long, puberulous, lower lobe cucullate, 9--10 mm long, the other four lobes 8--9 mm long, appressed silky puberulous on both surfaces, the margins frayed, and sometimes fimbriate glandular, all reflex at anthesis. *Corolla* yellow to pale tangerine, the outer surface of all five petals flushed orange and densely glandular with red or, less commonly yellowish-orange or yellowish-green, sessile or short-stalked, mushroom-shaped glands in the central-basal portion of the blade; standard petal speckled orange-scarlet on inner surface or not, the blade orbicular, suborbicular or obovate-elliptic, 1.2--1.7 x 0.8--1.3 cm (including a 2--3 mm claw), the thickened claw densely pubescent especially on the margins, a large, pubescent folded appendage, flange or indented ridge at the claw apex; upper lateral petals with a depressed-orbicular to obovate blade, apex emarginate, 1.2--1.9 x (0.8--)1.2--1.85 cm (including a 1--2.5 mm claw), the claw densely pubescent on the inner surface, the margins with stipitate mushroom-shaped glands or gland-tipped protuberances; lower lateral petals with an orbicular to obovate blade, apex emarginate, 1.3--1.9 x 0.8--1.5 cm (including a 2--3.5 mm claw), the claw moderately pubescent or glabrous and with stalked, mushroom-shaped glands on the margins. Stamen filaments yellow, 1.4--1.6(--2.1) cm long, densely white lanate on the lower $^1/_2$--$^2/_3$, the hairs thinning out towards the apex, occasionally a few short-stalked glands visible amongst the hairs; anthers brown, 2--2.5 x 1 mm. Ovary densely pubescent with matted white hairs, eglandular or sparsely glandular,(4--)5--6(--7)-ovulate; style 1.3--1.7 cm long, pubescent on the lower ½ or glabrescent, widening towards apex; stigma a terminal, tubular or funnel-shaped, fringed chamber (the fringe cells fused). *Fruit* an explosively dehiscent, thinly woody, straight or falcate pod, 8--12.5 x (1.7--)2--2.8 cm, finely puberulous over whole surface but most evident on upper margin or glabrous, eglandular

or with dark red, short-stalked, pixie-cup glands intermixed with the pubescence, (2--)3--5-seeded, hypanthium of calyx persisting as ring at fruit base.

Seeds yellow, ochre-buff or brown, shiny, subcordate, suborbicular or ovate, 10--12 x 9--12 x 1.5--2 mm. *Seedling* germination phaneroepigeal, first eophyll with 3 opposite pairs of leaflets, second eophyll bipinnate with one opposite pair of pinnae plus a terminal pinna, each pinna with 2 pairs of opposite leaflets.

13a. subsp. **yucatanensis**

Caesalpinia recordii Britton & Rose in Trop. Woods 7: 6 (1926).

Type: Belize, Feb. 1926, *Record* s.n. (holotype US, isotypes F!, GH!, NY!).

Poincianella yucatanensis (Greenman) Britton & Rose in N. Amer. Fl. 23(5): 330 (1930).

Poincianella recordii (Britton & Rose) Britton & Rose in N. Amer. Fl. 23(5): 329 (1930).

Standard petal blade inner surface speckled orange-scarlet centrally, outer surfaces of all petals densely glandular with red (rarely yellowish) glands, apex of standard claw with a pubescent folded appendage, flowers about as wide as long.

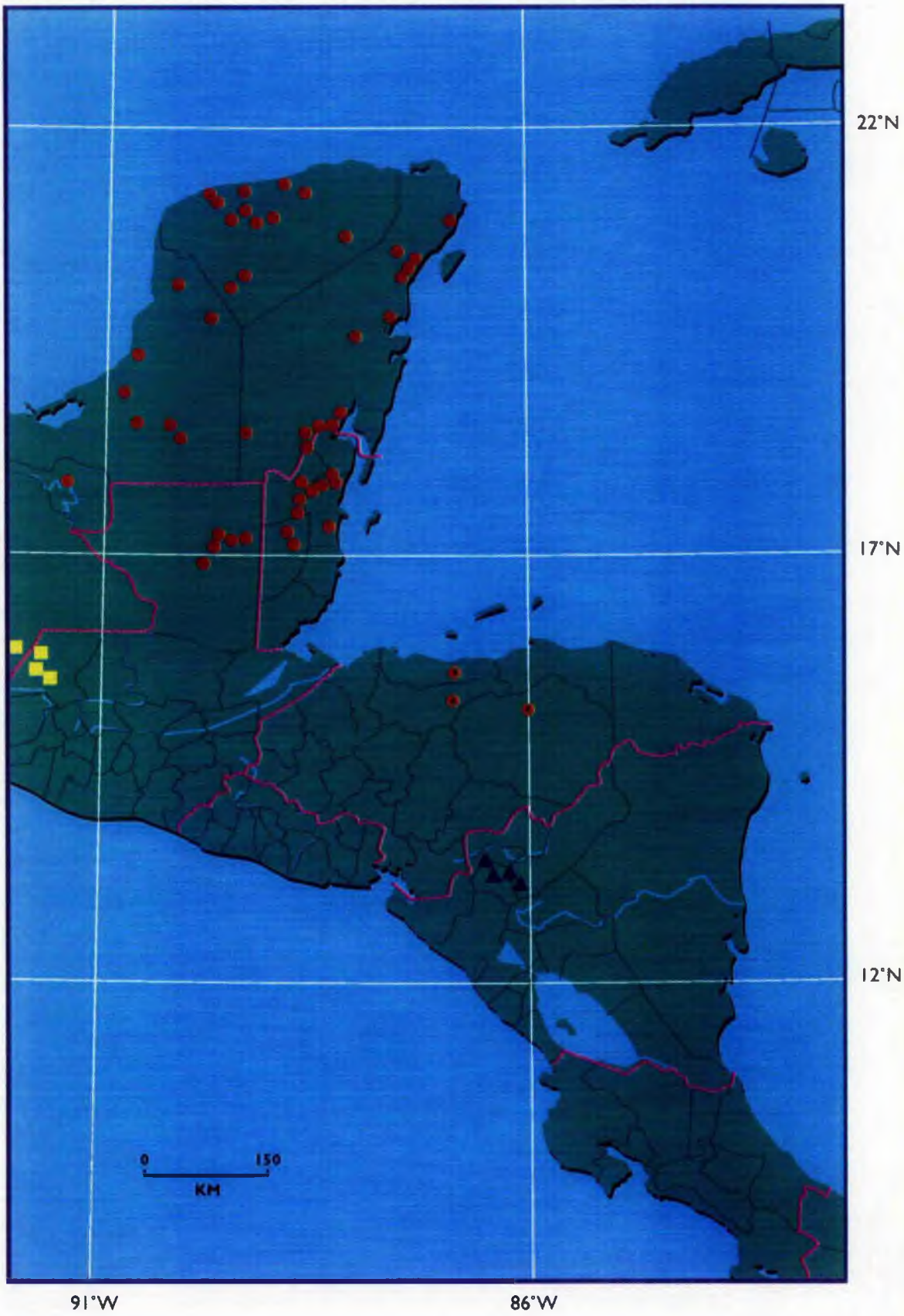
(Fig. **27**, Map 12).

DISTRIBUTION. Belize, the Yucatan peninsular of Mexico and north eastern Guatemala in the Department of Péten.

MEXICO: Yucatan, 1895 *Armour* 75 (F!); 9 Jan. 1979, *Bradburn & Darwin* 1132 (F!); Dzibilchaltun, 14 Jan. 1979, *Bradburn & Darwin* 1252 (MEXU!, MO!); Oxkutzcab, April 1943, *Bruff* 1498 (MEXU!); between Xul and Benito Juarez, 11 Jan. 1983, *Darwin* 2513 (MEXU!, NY!); 3 km W of Tixkokob, 2 Jan. 1982, *Darwin & Sundell* 2089 (EAP!, F!); 3 km E of Hoctun, 2 Jan. 1982, *Darwin & Sundell* 2106 (MEXU!); WNW of Chuchola, Dec. 1955, *Enriquez* 271 (MEXU!); Progresso, 1935, *Flores* s.n. (F!); Izamal, 1895, *Gaumer* 371 (holotype F!, isotypes K!, NY!); Jan. 1917, *Gaumer et al.* 23521 (F!, GH!); 1916, *Gaumer* 23201 (F!); without exact date, *Gaumer* 24142 (F!); without date, *Gaumer* 1715 (F!); Itzima, 19 Feb. 1906, *Greenman* 335 (F!, GH!, NY!); 20 Feb. 1906, *Greenman* 349 (F!); near Izamal, 22 Feb. 1906, *Greenman* 417 (F!); 25 km N of Valladolid, 2 Feb. 1985, *Hughes* 493 (K!, MEXU!); farmstead of Unidad Juarez on highway 14 from Tizimin to Buctzotz, 5 March 1989, *Lewis & Hughes* 1765 (FHO!, K!, MEXU!, NY!); N of Izamal, 5 March 1989, *Lewis & Hughes* 1766 (BR!, FHO!, K!, MEXU!, NY!); 1895, *Millspaugh* 75 (F!); Progresso, 5 March 1899, *Millspaugh* 1660 (F!); near Hoctun, 30 Jan. 1960, *Saunders*

FIG. 27. *Caesalpinia yucatanensis* subsp. *yucatanensis*. **A** part bipinnate leaf x 1; **B** median leaflet undersurface x 1; **C** median leaflet undersurface to show size range x 1; **D** bark section from young branchlet x 1½; **E** bark section from older branch x 1½; **F** tip of young inflorescence showing bracts x 1; **G** inflorescence x 1; **H** calyx opened out x 3; **J** standard petal x 4½; **K** outer surface of lower lateral petal x 4½; **L** stamen x 4½; **M** gynoecium x 4½; **N** stigma x 24; **P** developing ovary x 1; **Q** fruit x 1; **R** detail of fruit valve glands x 30; **S** seed x 1½; **T** seedling x 1. **A & B** from *Lewis & Hughes* 1758, **C** from *Lewis & Hughes* 1760, **D, E & Q–T** from *Lewis & Hughes* 1765, **F & H–N** from *Lewis & Hughes* 1759, **G & P** from *Lewis & Hughes* 1761. Drawn by Sue Wickison.

Distribution of *Caesalpinia yucatanensis* subsp. *yucatanensis* (●) subsp. *hondurensis* (●) subsp. *chiapensis* (□) and *C. nicaraguensis* (▲) in Mexico and Central America.



225 (US!); Mérida, 1865, *Schott* s.n. (F!); Mérida, 11 Feb. 1903, *Seler & Seler* 3844 (F!); 35 km from Valladolid on road to Puerto Juarez, 18 Feb. 1958, *Schubert & Gomez Pompa* 1628 (MEXU!); between Mérida and Chichen-Itzu, 27 March 1970, *Utley* 8--27 (NY!); 1896, *Valdez* 7 (in part) (F!); Yokdzonot Presentados, 16 April 1986, *Zepeda et al.* 190 (MEXU!); **Quintana Roo**, 17 Jan. 1981, *Cabrera & Torres* 1037 (MEXU!); 8 km S of San José, 17 Feb. 1981, *Cabrera & Torres* 1241 (MEXU!); 4 km E of Dos Aguadas, 22 Dec. 1982, *Cabrera & Cabrera* 4166 (MEXU!); 8 km S of Akumal, 13 March 1981, *Cabrera & Zarate* 1469 (MEXU!); 7 km S of Akumal, 17 Dec. 1982, *Cabrera & Cabrera* 4003 (MEXU!); 3 km N of Crema de Xel-Ha, 6 Dec. 1980, *Cabrera & Durán* 562 (MEXU!); 11 km SE of the diversion to Churmpon on new road to Vigía Chico, 18 Dec. 1982, *Cabrera & Cabrera* 4031 (MEXU!); 16 km S of Tres Garantias, 26 April 1982, *Cabrera & Cabrera* 2533 (K!, MEXU!); 7 km N of Chetumal, 19 March 1983, *Cabrera & Godinéz* 4491 (MEXU!); 2 km E of Calderitas, 18 March 1981, *Cabrera & Zarate* 1580 (MEXU!); 1 km S of Ejido Caobas, 20 March 1981, *Cabrera & Alvarez* 1616 (MEXU!); Mpio. Carrillo Puerto, 10 km SE of Crucero de Chumpon, 15 Feb. 1984, *Durán & Olmsted* 805 (MEXU!); Mpio. Carillo Puerto, 13 Jan. 1984, *Durán & Olmsted* 735 (MEXU!); 4 Feb. 1984, *Durán & Olmsted* 866 (MEXU!); 15 km NW of Chetumal, 22 April 1981, *Grether & Quero* 1565 (MEXU!); highway 307, Chetumal to Filipe Carillo Puerto, 4 March 1989, *Lewis & Hughes* 1761 (BR!, FHO!, K!, MEXU!, NY!, US!); 30 km W of Chetumal, 13 March 1992, *MacQueen* 478 (EAP, FHO, K!, MEXU); km 160 Merida to Valladolid, 18 Jan. 1976, *Moreno* 397 (MEXU!); between Playa Aventura and Akumal, 1 March 1976, *Moreno* 517 (MEXU!); zona arqueológica de Cobá, 2 March 1976, *Moreno* 529 (MEXU!); km 23 Chetumal to Solaguna, 6 March 1958, *Schubert & Gomez Pompa* 1707 (MEXU!); Playa del Carmen, 6 Jan. 1980, *Sousa* 10934 (MEXU!, MO!); road to Ingenio Alvaro Obregón, 16 km S of crossroads with Escárcega to Chetumal road, 5 March 1980, *Téllez & Cabrera* 1690 (MEXU!); 3 km N of Cobá, road to Nuevo Xcan, 3 Feb. 1980, *Téllez & Cabrera* 1397 (MEXU!); 9 km S of Andrés Quintana Roo, 12 Jan 1980, *Téllez & Cabrera* 1284 (MEXU!); 26 km N of Tulum, 9 Jan 1980, *Téllez & Cabrera* 1155 (MEXU!); 3 km S of Laguna Guerrero, 7 Feb. 1980, *Téllez & Cabrera* 1516 (MEXU!); Puerto Morelos, 20 Feb. 1984, *Uitzil et al.* 2 (MEXU!); **Campeche**, Playa Bonita, 1 April 1953, *Bravo* s.n. (MEXU!); environs of Escárcega, 9 Jan. 1953, *Bravo* 1214 (MEXU!); 4 km N of Pomuch, 23 Nov. 1986, *Cabrera & Cabrera* 12765 (MEXU!); 2 km E of Sta. Maria Xcabacab, 7 March 1982, *Cabrera et al.* 2067 (MEXU!); 70 km E of Escárcega, 26 March 1982, *Cabrera & Cabrera* 2243 (MEXU!); Mpio. Hopelchan, Xeochkax, 9 March 1987, *Labat* 1924 (MEXU!); Tuxpeña, 10 Feb. 1932, *Lundell* 1314 (F!, GH!, MO!, NY!); 29 Jan. 1932 *Lundell* 1265 (F!, GH!, MEXU!, NY!); Chan Laguna, 6 Dec. 1931, *Lundell* 1014 (F!, NY!); 3 km SW of Pomuch, 6 Feb. 1983, *Martínez et al.* 3022 (K!, MEXU!); Campeche, without date, *Perrine* s.n. (NY!); 10 km NNW of Felipe Carillo Puerto, 27 April 1978, *Quero & Grether* 966 (MEXU!); 0.5 km S of Xpujil, 13 Feb. 1973, *Shepherd* 67 (F!, LL!); 2 km E of Conhuas, 3 Feb. 1983, *Téllez et al.* 6288 (MEXU!); **Tabasco**, Mpio. of Balancan, 2 April 1976, *Calzada* 2344 (F!, MEXU!, TEX!); 500 m from the frontier with Campeche, 2 Nov. 1976, *Menendez et al.* 428 (K!, MBM!, MEXU!, MO!, TEX!); **BELIZE**, El Cayo, 5--13 March 1931, *Bartlett* 11974 (F!); Hillbank, March 1929, *Brown* 36 (F!); El Cayo, March-June 1933 *Chanek* 87 (F!); March-June 1933, *Chanek* 100 (F!); Orange Walk District, road between Lamanai and San Felipe, 19 March 1987, *Davidse & Brant* 32719 (K!); 10--15

miles W of Belize City, without date, *Dwyer* 5--75 (MO!); mile 19, northern highway, 25 Jan. 1974, *Dwyer & Liesner* 12238 (MEXU!, MO!, US!); mile 21, northern highway, 19 Jan. 1974, *Dwyer & Leisner* 12047 (MEXU!, US!); El Cayo District, 5 March 1938, *Gentle* 2309 (A!, K!, MEXU!); Maskall Pine Ridge, Jan. 1934, *Gentle* 1106 (F!, GH!, K!); without date, *Gentle* 176 (F!); Hillbank Camp, Feb. 1933, *Pelly* 39 (F!); 1926, *Record* s.n. (F!, GH!, NY!, US); Boston, 5 km N of Sand Hill on northern road, 4 Dec. 1981 *Sousa et al.* 12202 (MEXU!, MO!); Santa Martha, 21 km SE of Orange Walk, 4 Dec. 1981, *Sousa et al.* 12206 (MEXU!); without date, *Winzerling* VIII--4 (F!); **GUATEMALA, Dept. of Petén**, Santa Cruz, 27--28 March 1931, *Bartlett* 12405 (F!); San Clemente to Dos Arroyos, 1 May 1931, *Bartlett* 12837 (F!); Tikal National Park, 31 Jan. 1969, *Contreras* 8327 (F!, K!, LL!, MEXU!, NY!); 23 Jan. 1964, *Contreras* 3921 (LL!, MEXU!, NY!); 18 Feb. 1961, *Contreras* 1965 (LL!, K!, MEXU!); 36 km NE of Tikal, Bajo de Santa Fe, 3 Feb. 1960, *Contreras* 592 (F!, LL!, MEXU!); Tikal National Park, 1 March 1989, *Lewis & Hughes* 1758 (BR!, FHO!, K!, MEXU!, NY!); c 15 km N of Santa Elena, 2 March 1989, *Lewis & Hughes* 1759 (FHO!, K!, MEXU!, NY!); *Lewis & Hughes* 1760 (FHO!, K!, MEXU!, NY!); Tikal, 1 March 1961, *Lundell* 16822 (F!, LL!, MEXU!); 20 Feb. 1959, *Lundell* 15690 (LL!, MEXU!); Bajo de Santa Fe, Rio Holmul, 16 Feb. 1959, *Lundell* 15593 (LL!, MEXU!); Peten, road from Flores to Tikal, 24 Jan. 1991, *MacQueen & Pennington* 82 (EAP, FHO, K!, MEXU, MO); 47 km from Santa Elena on road to Remate, 12 March 1970, *Ortíz* 742 (EAP!, F!); 20 Jan. 1972, *Ortíz* 2199 (EAP!).

ECOLOGY. Low deciduous woodland; semi-evergreen dry thorn forest and scrubby woodland, 15--500 m.

PHENOLOGY. Flowering from November to March, fruiting from January to April.

VERNACULAR NAMES. "Xkanpocolcum", "Kanpococum" (Mexico, Yucatan); "Caramayo" (Belize).

NOTES. The long, straight poles are used in house construction (*Gaumer et al.* 23521) and the wood is valued for cabinet making (*Winzerling* VIII-4).

13b. subsp. **chiapensis** *G.P. Lewis*, subsp. nov., in sched. Type: Mexico, Chiapas, c 4 km from Comalapa on road to La Trinitaria, 27 Feb. 1992, *Hughes et al.* 1684 (holotype K!, isotypes E, FHO, MEXU, MO, NY).

Standard petal blade inner surface without orange speckling, outer surfaces of all petals with yellow or yellowish-green glands, apex of standard claw with an unfolded pubescent flange, flower about as wide as long. (Figs. 9C & 28C, Map 12).

DISTRIBUTION. Mexico in eastern Chiapas and just over the border in Guatemala.

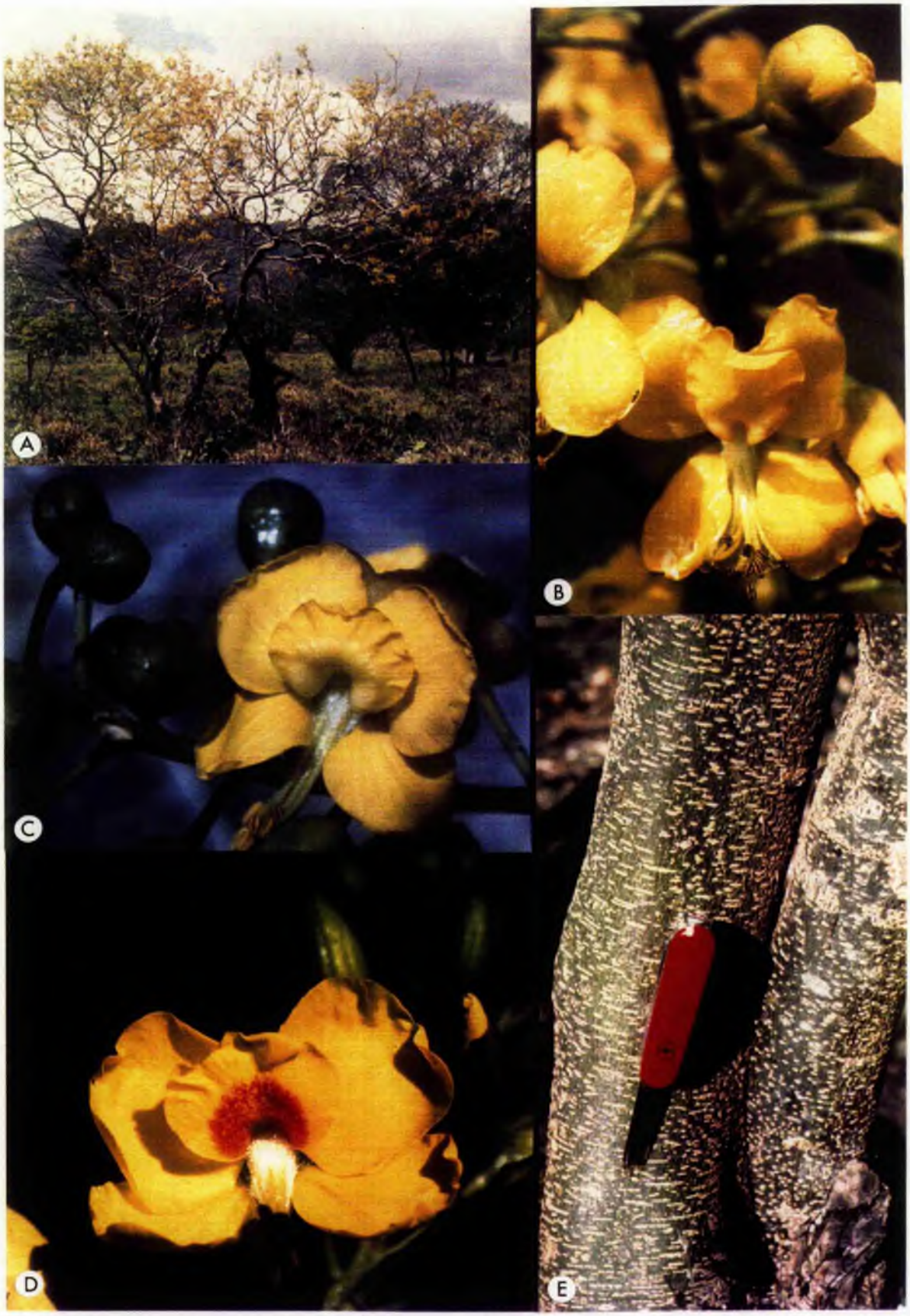


FIG. 28. *Caesalpinia yucatanensis* subsp. *hondurensis*: **A** habit (*Hughes* 1448, type); **B** flowers (*Hughes* 1448); *C. yucatanensis* subsp. *chiapensis*: **C** flower (*Hughes* 1354); *C. nicaraguensis*: **D** flower (*Hughes* 1406, type); **E** bark (*Hawkins* 4). All photographs by C.E. Hughes.

MEXICO: Chiapas 6--8 km E of Frontera Comalapa along road to Ciudad Cuauhtémoc, 29 Feb. 1972, *Breedlove* 24257 (MEXU!, NY!); c 20 km from Ciudad Cuauhtémoc, 1 April 1989, *Hughes* 1353 (K!); c 4 km from Comalapa, 27 Feb. 1992, *Hughes* 1684 (K!); **GUATEMALA**, Huehuetenango, c 6 km N of Camoja Grande, 2 April 1989, *Hughes* 1354 (K!).

ECOLOGY. Degraded dry tropical deciduous forest, 630--705 m.

PHENOLOGY. Flowering February to April, fruiting in April.

NOTES. The subspecies is a locally frequent, narrowly restricted endemic with strongly scented flowers. It differs from subsp. *yucatanensis* by its pure yellow flowers, yellowish-green floral glands, less pronounced standard claw appendage and occurrence at higher altitudes, and from subsp. *hondurensis* by its broader, more robust flowers.

13c. subsp. **hondurensis** G.P. Lewis subsp. nov., in sched. Type: Honduras, Dept. Yoro, lower Aguan Valley, c 31 km W of Olanchito, 25 March 1991, *Hughes* 1448 (holotype K!, isotype FHO).

Standard petal blade inner surface without orange speckling, petal glands yellow, apex of standard claw with a pubescent ridge, flowers longer than wide. (Fig. 28A & B, Map 12).

DISTRIBUTION. Honduras.

HONDURAS: Olancho, by the Rio Grande on San Esteban to Gualaco road, 17 Feb. 1982, *Blackmore & Heath* 1866 (MEXU!); Dept. Yoro, lower Aguan Valley, c 31 km W of Olanchito, 12 km E of San Lorenzo, near San Jeronimo on N side of Rio Aguan, 25 March 1991, *Hughes* 1448 (FHO, K!); Dept. Atlantica, La Ceiba, Coyole's yard, 9 March 1949, *Molina & Becker* 6 (EAP!, F!).

ECOLOGY. Slightly disturbed dry thorn scrub, 220 m.

PHENOLOGY. Flowering in February and March, fruits developing in late March.

VERNACULAR NAME. "Berberillo".

NOTE. Differing from the other two subspecies by its flowers being proportionately longer than wide.

14. **Caesalpinia nicaraguensis** *G.P. Lewis* sp. nov., in sched. Type: Nicaragua, Department of Esteli, *Hughes* 1406 (holotype MEXU!; isotypes EAP, FHO,K!, NY!).

Single or multiple-stemmed, unarmed small tree 3--9 m tall with spreading crown; bark smooth, grey-brown to mid greenish-brown, speckled with light brown to orange, elliptic to orbicular, raised lenticels, inner bark light green; branchlets puberulous with scattered golden-brown stellate hairs intermixed, glabrescent. *Leaves* bipinnate; stipules ovate, 2.5--5 x 2--3 mm, moderately to densely pubescent on outer surface, early caducous; petiole 1.5--3.5 cm long, moderately pubescent along upper edge and on pulvinus, glabrescent; rhachis 1.2--4.5 cm long, pubescent with white hairs; pinnae in 2--4 opposite pairs (the basal pair sometimes alternate) plus a terminal pinna; leaflets in 5--7 opposite pairs per pinna, petiolulate, the pubescent petiolule 0.5--1 mm long, discolorous, dark bottle green and slightly glossy above, paler below, oblong-elliptic to obovate, apex rounded or retuse, base slightly inequilateral about the main vein, margin thickened, slightly revolute, 1.3--1.8 x 0.6--1 cm (terminal leaflets), 0.9--1.7 x 0.5--0.7 cm (median leaflets of middle pinnae), glabrous (sometimes a small tuft of hairs at base of midvein on lower surface) to sparsely puberulous, the main vein prominent on lower surface, secondary venation, where evident, brochidodromous, leaflet blades eglandular, short-stalked glands often present in axes of petiolules on lower surface of pinna rachis,dark, stipitate glands on very young foliage rachises, especially at the point of the pinnae insertion, the gland stalks plumose with white or hyaline hairs. *Inflorescence* an erect, terminal c 40--90-flowered raceme or multi-flowered panicle, main rhachis and pedicels densely golden tomentulose with scattered golden-brown stellate or plumose hairs intermixed; bracts ovate, acute, c 7 x 5 mm, tomentulose, early caducous; pedicels 9--12 mm long, articulated c 3 mm below calyx base. *Calyx* tube 2--4 mm long, the lower, cucullate lobe 10--13 mm long, the other four 8--11 mm long, outer surface of calyx densely golden tomentose, inner surface moderately to densely puberulous, sepal margins ± fimbriate with laxly spaced plumose

hairs. *Corolla* bright yellow; standard mottled bright orange at base, its blade obovate to suborbicular, apex rounded, 1.4--1.7 x 1.1--1.4 cm (including the 3 mm long claw), lower $^1/_2$--$^2/_3$ of outer surface glandular with closely packed, sessile or short-stalked, mushroom-shaped glands, the thickened claw densely pubescent on the margins, a thickened hairy ridge at the apex of the claw on the inner surface; upper lateral petals with a suborbicular to subcordate, shallowly emarginate blade, this eglandular but for the sessile glands on the lower $^1/_3$ of the margin, 1.8--2 x 1.5--1.7 cm (including the 3 mm claw), the claw moderately pubescent on the inner surface, glandular or not on the outer surface, densely pubescent on the margins with stipitate, pixie-cup glands intermixed; lower lateral petals with an obovate to subcordate, shallowly emarginate blade, this eglandular but for the sessile glands on the lower $^1/_3$--$^1/_2$ of the margin, 1.8--2 x 1.1--1.4 cm (including the 2.5--3 mm claw), the claw as for the upper lateral petals but less pubescent. Stamen filaments arcuate, 1.6--1.7 cm long, densely white-lanate on lower $^1/_2$, sparsely pubescent towards apex; anthers dorsifixed, dark olive-green, 2 x 0.75 mm. Ovary densely golden tomentose, eglandular or with a dense covering of sessile and short-stalked, shallow pixie-cup glands intermixed with the hairs; style arcuate, 1.5--1.6 mm long, the lower $^1/_2$ densely tomentulose; stigma tubular, terminal, fringed. *Fruit* a dehiscent, woody pod, 5.8--7.8 x 1.9--2.2 cm, puberulous and eglandular or with dark red, stalked pixie-cup glands mixed with the indumentum, the glands thin or thick stalked, both types with the stalks pubescent, a red secretion exuded from the glands makes the young fruits sticky, 3--4-seeded. (Figs. 8B, 28D & E & **29**, Map 12).

DISTRIBUTION. Endemic to Nicaragua.

NICARAGUA. Dept. Madriz, Sipián, road Somoto to Cusmapa, 9 Aug. 1984 *Hernández et al.* 670 (NY!); Dept. Esteli, c 24 km NNW of Esteli, 86°27'W, 13°10'N, 8 Feb. 1991, *Hughes* 1406 (holotype MEXU!, isotypes EAP, FHO, K!, NY); 18 km from Jinotega on road to Yali, 86°07'W, 13°15'N, 21 March 1991, *MacQueen & Styles* 72 (EAP, FHO, K!, MEXU, MO); between La Sabana and Cusmapa, 14 March 1967, *Molina* 20596 (F!, NY!, US!); Dept. Jinotega, trail between Jinotega and Las Mesitas, 21 June 1947, *Standley* 9746 (F!).

ECOLOGY. Mixed pine-oak forest and oak forest with *Mimosa* and *Acacia pennatula* common. 1100--1400 m.

FIG. 29. *Caesalpinia nicaraguensis*. **A** inflorescence and bipinnate leaf x 1; **B** leaflet undersurface x 3; **C** section of bark x 1½; **D** bract x 4½; **E** calyx opened out x 3; **F** standard petal x 3; **G** l.s. of standard petal base x 6; **H** upper lateral petal x 3; **J** lower lateral petal x 3; **K** stamen x 4½; **L** gynoecium x 4½; **M** stigma x 30; **N** immature fruit x 1; **P** mature fruit (glands worn off) x 1. **A–N** from *Hughes* 1406, **P** from *Molina* 20596. Drawn by Eleanor Catherine.

PHENOLOGY. Limited data available but collected in flower in February, March and August and in fruit February, March and June.

VERNACULAR NAME. "Malincha" (*MacQueen & Styles* 72).

NOTES. *C. nicaraguensis* appears to be most closely related to *C. yucatanensis* and *C. acapulcensis* but differs from both by the larger number of leaflets per pinna (5--7 opposite pairs) and the smaller leaflets (the terminals up to 1.8 x 1 cm). In addition the species differs from *C. acapulcensis* in having the ridge at the apex of the standard claw pubescent rather than glabrous and from *C. yucatanensis* by its shorter pedicels and fruits. *C. acapulcensis* comes from the west coast of Mexico (in the states of Jalisco, Colima, Michoacan and Guerrero); *C. yucatanensis* from the Yucatan Peninsula of Mexico and the Department of Péten in NE Guatemala, with subspecies *chiapensis* in the Mexican state of Chiapas and just into Guatemala, and subspecies *hondurensis* in Honduras. *C. nicaraguensis* is endemic to Nicaragua.

15. **Caesalpinia laxa** *Benth.*, Pl. Hartw.: 60 (1840). Type: Mexico, Oaxaca, Teojomulco, *Hartweg* 455 (holotype BM!, isotypes E!, K!, photos F!, MEXU!).
Poincianella laxa (Benth.) Britton & Rose in N. Amer. Flora 23(5): 329 (1930).

Unarmed shrub, 0.5--1 m tall, stems finely pubescent to glabrous. *Leaves* bipinnate; petiole 2.7--4.3 cm long, pubescent or glabrous; rhachis (lacking--)2--8.5 cm long, pubescent or glabrous, pinnae in (1--)2--5 opposite pairs, plus a terminal pinna; leaflets in (2--)3--9 opposite pairs, elliptic to obovate, apex obtuse, rounded or retuse, base oblique, margin slightly thickened, revolute, terminal leaflets 5--9(--21) x 2.5--4(--10) mm, median leaflets 7--8(--16) x 2.5--4(--9) mm, upper surface glabrous or very sparsely pubescent, lower surface glabrous to moderately pubescent; venation obscure, only the main vein prominent on the lower surface, leaflets eglandular or with a few punctate glands along margin, a corona of prickle-like structures around the pinnae insertions, these sometimes gland-tipped, usually one prickle-like structure at base of each leaflet pulvinule on lower surface, similar structures sometimes scattered along petiole of leaf. *Inflorescence* an axillary or terminal 10--35-flowered raceme, the rhachis and pedicels glabrous; bracts ovate-acuminate, 4--4.5 x 2--2.5 mm, margins ciliate; pedicels slightly to strongly

deflexed (the flowers ± nodding at anthesis), 8--11 mm long, articulated 1--2 mm below pinkish-red calyx. Hypanthium 3--4 mm long, ribbed, lower calyx lobe cucullate, 7--8 mm long, other lobes 5--7.5 mm long, all with outer surfaces glabrous, inner surfaces pubescent and margins ciliate. *Corolla* yellow tinged pink; standard petal blade elliptic, 6.5--8 x 4.5--7 mm (including a 1.5 mm claw), inner surface glabrous, eglandular and lacking a ridge, the claw unelaborated, outer surface with stalked glands at base of blade; upper lateral petals broadly triangular-cordate, apex obtuse to rounded, c 7--8 x 5--6 mm (including a 0.5 mm claw), blade with 1--2 marginal vesicles (fide Contreras); lower lateral petals broadly elliptic, c 7--8 x 4.5--7 mm (including a 0.5 mm claw), all lateral petals glabrous and eglandular on both surfaces. Stamen filaments 12--17 mm long, well exserted from petals, white pubescent on basal $^1/_4$--$^1/_3$, alternate stamens glandular with stipitate glands scattered along entire length of filament; anthers 1--1.5 x 0.5--1 mm. Ovary densely white lanate with curved, interwoven hairs, stipitate, stipe 0.5--0.7 mm long; style 10--16 mm long, pubescent on basal $^1/_3$--$^1/_2$, curved at apex; stigma a terminal, tubular, unfringed chamber. *Fruit* an elastically dehiscent, subligneous pod, 5--7 x 1.2--1.5 cm, pubescent, short-stipitate, the stipe 1 mm long, 1--2-seeded. *Seeds* dark brown, ovate, 7.4--8.6 x 6.3--7.7 x 2--2.2 mm. (Fig. 30, Map 7).

DISTRIBUTION. Mexico in the Sierra Madre del Sur from Omiltemi in Guerrero to Teojomulco in Oaxaca.

MEXICO: Guerrero, Mpio. Zitlala, 7 km N of Santa Cruz on road to San Juan Las Joyas, 29 Sept. 1987, *Contreras* 2112 (K!, MEXU!); same locality and date, *Contreras* 2119 (K!, MEXU!); 5 km N of Santa Cruz, 16 Oct. 1987, *Contreras* 2183 (MEXU!); between Tixtla and Chilapa, 5 Aug. 1978, *Germán et al.* 967 (MEXU!); 2 miles E of Amajilica, 1 July 1954, *Herald & Clark* 436 (TEX!); 4 miles W of Chilpancingo, 18 June 1953, *Richards & Rowell* 3349 (TEX!); **Oaxaca,** Teojomulco, without date, *Hartweg* 455 (holotype BM!, isotypes E!, K!, photos F!, MEXU!).

ECOLOGY. Open areas of tropical deciduous woodland, 1400--2000 m.

PHENOLOGY. Flowering July to November, fruiting August to November.

NOTES. *Hartweg* 455, the type of the species and only known collection from Oaxaca has more pinnae per leaf and more leaflets per pinna (7--8 pairs) than material from Guerrero (2--3 pairs of leaflets per pinna). More material is needed from Oaxaca to see if

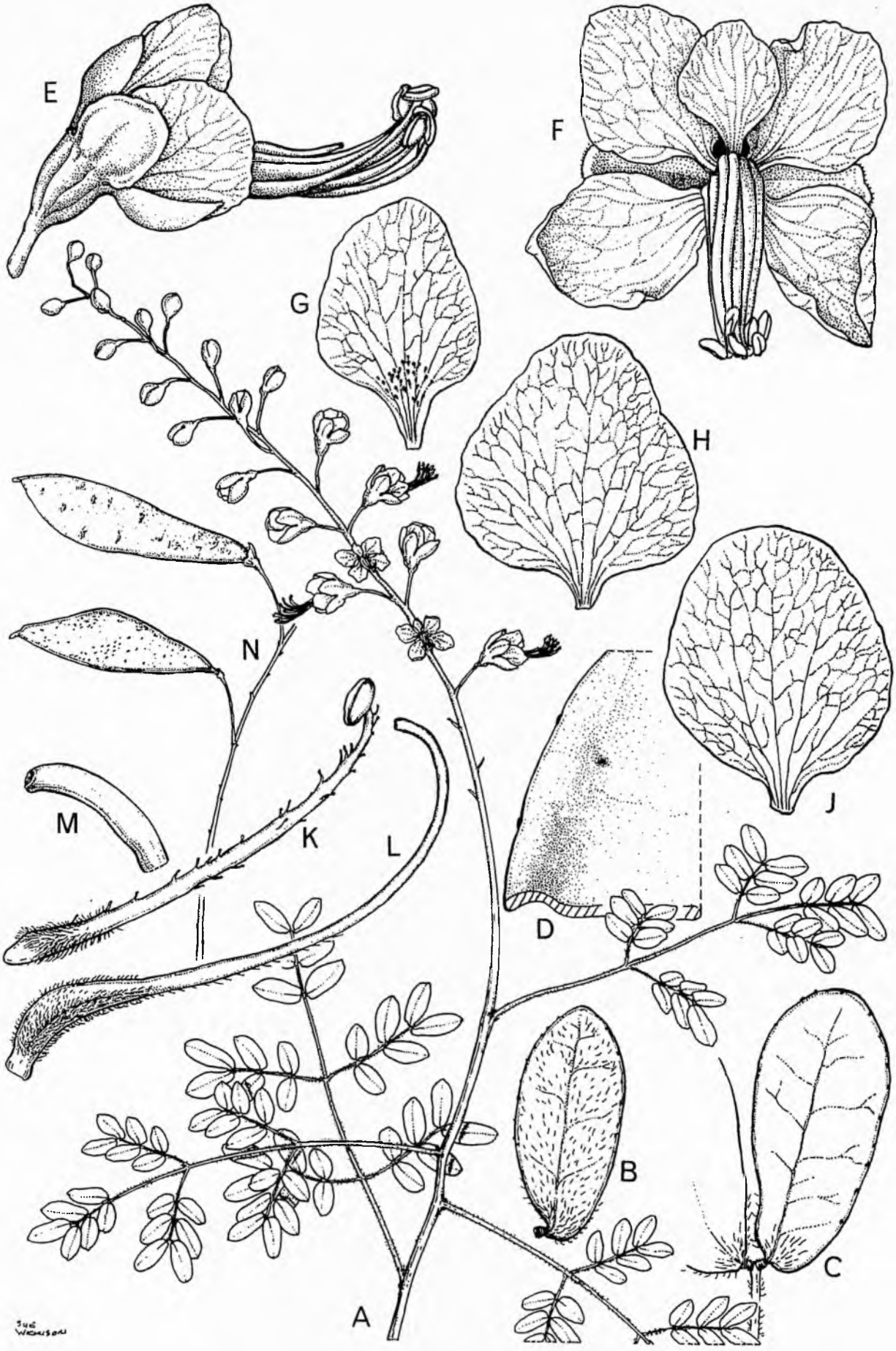


FIG. 30. *Caesalpinia laxa*. **A** inflorescence and foliage x 1; **B** terminal leaflet undersurface x 6; **C** terminal leaflet upper surface x 6; **D** part of leaflet margin showing glands x 21; **E** flower side view x 4½; **F** flower front view x 4½; **G** standard petal dorsal surface with glands x 9; **H** upper lateral petal x 9; **J** lower lateral petal x 9; **K** stamen x 9; **L** gynoecium x 9; **M** stigma x 21; **N** fruits x 1. **A** & **E–M** from *Contreras* 2119, **B–D** & **N** from *Contreras* 2112. Drawn by Sue Wickison.

this difference in leaf formula is consistent and possibly worthy of recognition at infraspecific rank.

16. **Caesalpinia hintonii** *Sandwith* in Kew Bull. 1937: 303 (1937). Type: Mexico, Guerrero, District of Coyuca, Cuajilote, 9 May 1935, *Hinton* 7746 (holotype K!, isotypes A!, F!, GH!, MEXU).

Small, unarmed tree, 2--7 m tall, DBH up to 45 cm; bark greyish-white, exfoliating, occasionally corky; young stems reddish, glabrous. *Leaves* bipinnate; stipules ovate-lanceolate, acuminate, 2--6 mm long, pubescent, margins glandular-fimbriate, caducous; petiole 4--6(--10) cm long, glabrous or sparsely pubescent near apex, sometimes stipitate-glandular; rhachis (2.5--)9--10(--14.5) cm long, glabrous or sparsely pubescent; pinnae in 3--6 opposite pairs, usually plus a terminal pinna; leaflets in (3--)4--6(--10) opposite pairs, petiolules 0.5--1 mm long, blades oblong-elliptic to obovate, apex rounded to obtuse, base asymmetric (especially on terminal leaflets), 6--19(--25) x 3--10(--13) mm, young leaflets usually densely pubescent, mature ones pubescent or glabrous; venation obscure, secondary veins brochidodromous, main vein terminating in a dark glandular tip, leaflet blade eglandular or the margin with scattered, punctate glands, small glandular appendages at pinnae and leaflet insertions. *Inflorescence* a multi-flowered, erect or pendulous raceme up to 60 cm long usually aggregated into a terminal or axillary panicle, rhachis densely pubescent to glabrous; bracts ovate-lanceolate, acuminate, 2--5 mm long, pubescent, the margins glandular; pedicels (5--)7.5--15(--17) mm long, articulated 2.5--7 mm below the calyx, glabrous or pubescent, sometimes densely stipitate-glandular, the lower portion persisting on the rhachis after flower abscission, twisted (the flower resupinate) on pendulous racemes. *Calyx* tube ± ribbed, the lobes 4--9 mm long, glabrous or their margins ciliate, eglandular or with stipitate yellow glands (these drying red). *Corolla* salmon pink (? the petals rarely yellowish); standard petal blade ovate, apex acute, reflexed, 4.5--8.5 x 4--5.5 mm (including a 1--3 mm claw), the claw sigmoid in side view, a small tuft of hairs or a hairy u-shaped, thickened ridge at its apex on the inner surface at the point of reflexion of the blade, sparsely glandular on dorsal surface at apex; upper lateral petals broadly elliptic, 6--8 x 4.5--6.5 mm (including a 0.5--1.5 mm claw);

lower lateral petals 7.5--8.5 x 4--5.5 (including a 0.75--2 mm claw); all four lateral petals with a few stalked glands on basal $^1/_4$--$^1/_3$ of blade margin, the claws sparsely to moderately pubescent. Stamen filaments falcate, 6.5--11 mm long, white pubescent on basal $^1/_2$--$^3/_4$, stipitate-glandular on upper $^1/_4$--$^1/_2$ above zone of pubescence; anthers c 2 x 1 mm. Ovary pubescent, glandular (sometimes rudimentary, the flowers then perhaps functionally male), 1--3-ovulate; style 8--10 mm long (or 2.5--4 mm long on rudimentary gynoecium); stigma a terminal, tubular, unfringed chamber. *Fruit* a falcate, scimitar-shaped, chartaceous to subligneous, elastically dehiscent pod, 4.3--6 x 1.2--1.7 cm, pubescent or glabrous, eglandular or glandular with red, stipitate pixie-cup glands on basal $^1/_5$--$^1/_4$ or scattered over most of valve surface or with lime green, sessile, doughnut-shaped glands on the basal $^1/_2$, 1--3-seeded. *Seeds* pale fawn-brown or greyish brown, shiny, ovate-cordate, 9--11 x 6--10 x 2--2.5 mm. (Figs 2D, **31**, 32A-C & E, Map 7).

DISTRIBUTION. Mexico in Puebla, Michoacan and Guerrero, endemic to the Depression of the Rio Balsas.

MEXICO: Michoacan, San Antonio de Las Huertas, Mpio. of Nocupétaro, road to Villa Madero, 29 March 1982, *Núñez & Silva* 3905 (MEXU!); **Puebla**, Amatitlán, Izúcar de Matamoros, 7 Feb. 1978, *Huitrón* 16 (MEXU!); 20 km N of Acatlán de Osorio, 27. Jan. 1984, *Lemos* 878 (K!, MEXU!); Rancho Los Amantes, c 20 km SE of Izúcar de Matamoros, 18 Feb. 1965, *McVaugh* 22492 (MEXU!, NY!); 5 km W of San Bernado, Mpio. Ahuehuetitla, 12 Feb. 1977, *Sousa et al.* 7196 (K!); **Guerrero**, Mpio. La Union, 5 km S of Colmeneros, 13 June 1988, *Contreras* 2371 (K!); same locality and date, *Contreras* 2372 (K!); 2 km N of Tlalcoztitlan, Mpio. Copalillo, 20 Feb. 1986, *Contreras* 1850 (K!, MEXU)!; same locality and date, *Contreras* 1851 (K!) 1 km W of Atenango del Rio, on road to Huitzuco, 3 Feb. 1988, *Contreras* 2275 (K!); Mpio. Tepecoacuilco, 6 km E of San Juan Tetelcingo, 2 July 1987, *Contreras* 2038 (K!); Mpio. Coyuca de Catalan Zicuitaro, 22 km W of Santo Domingo on road to Santa Teresa, 7 March 1988, *Contreras* 2327 (K!); Mpio. Zumpango del Rio, 6 km E of San Juan Tetelcingo, 18 Feb. 1986, *Contreras* 1837 (K!); Mpio. Zumpango del Rio, 500 m E of Valerio Trujano, 31 Jan. 1988, *Contreras* 2261 (K!); Mpio. Coahuayutla, 12 km E of La Garita, 15 June 1988, *Contreras* 2388 (K!); Mpio. Tlapa, 4 km E of Tlapa on road to Igualita, 8 Feb. 1981, *Contreras* 807 (K!); Dist. Coyuca, Cuajilote, 29 Jan. 1934, *Hinton* 5567 (F!, K!, LL!); same locality, 9 May 1935, *Hinton et al.* 7746 (holotype K!, isotypes A!, F!, GH!, MEXU); 2 km SW of Mezcala, valley of Rio Xochipala, 26 Feb. 1987, *Hughes* 882 (K!, MEXU!); 56 km N of Chilpancingo, 10 Feb. 1992, *MacQueen et al.* 428 (EAP!, FHO!, K!, MEXU!); 22 km N of La Union, 13 Feb. 1992, *MacQueen & Nileshwar* 446 (EAP, FHO, K!, MEXU); c 35 km NNW of Chilpancingo, 3--5 km along road from Casa Verde to Xochipala, 2 Feb. 1965, *Mcvaugh* 22202 (NY!).

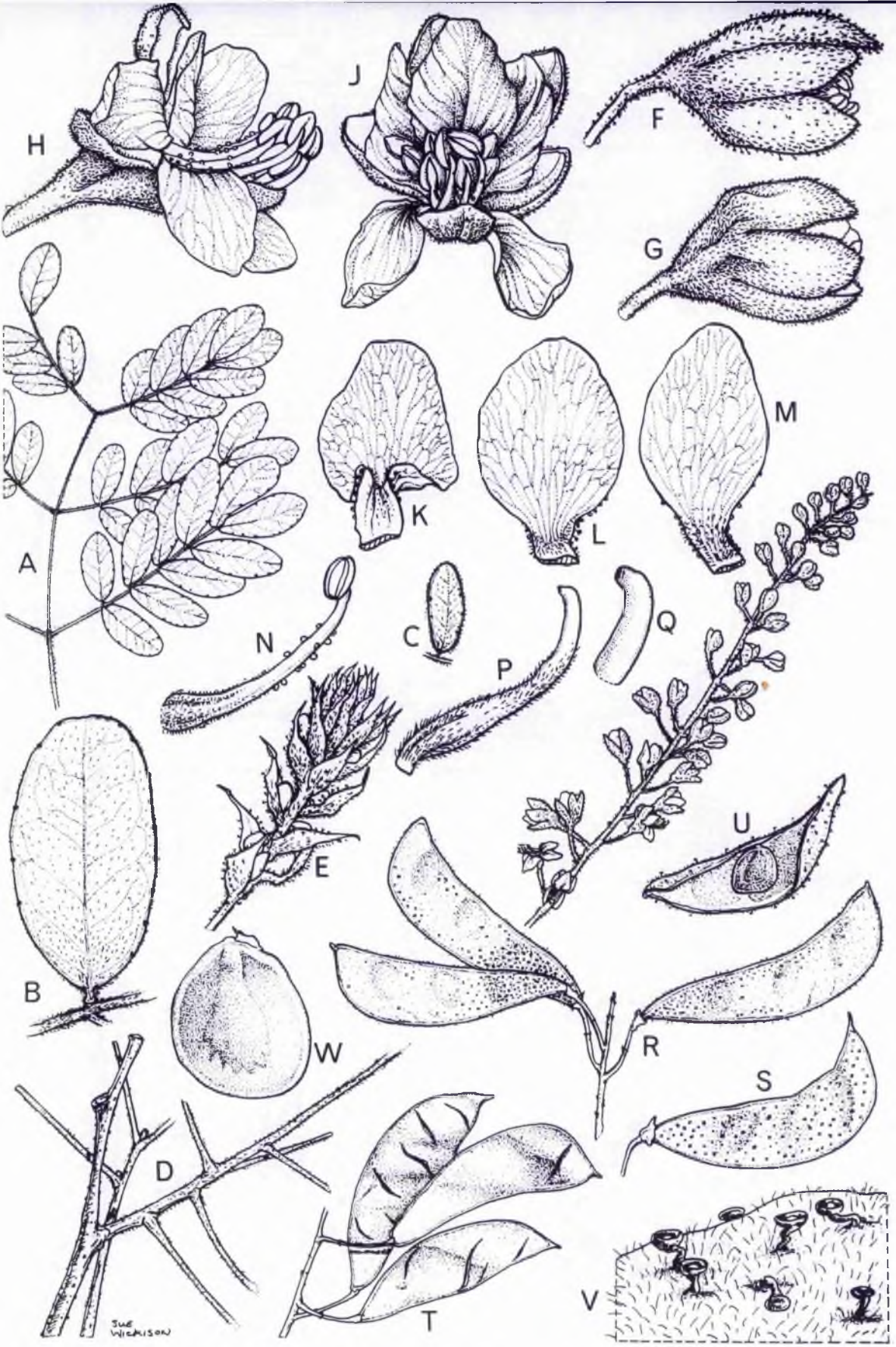


FIG. 31. *Caesalpinia hintonii*. **A** part bipinnte leaf x 1; **B** leaflet undersurface x 3; **C** smaller leaflet x 3; **D** inflorescence x 1; **E** bracts x 4½; **F** glandular bud x 4½; **G** eglandular bud x 4½; **H** flower side view x 4½; **J** flower front view x 4½; **K** standard petal x 6; **L** upper lateral petal x 6; **M** lower lateral petal x 6; **N** stamen x 6; **P** gynoecium x 6; **Q** stigma x 12; **R** fruits with few glands x 1; **S** glandular fruit x 1; **T** eglandular fruits x 1; **U** single valve of dehisced fruit x 1; **V** stalked glands on fruit surface x 12; **W** seed x 3. **A** & **B** from *Contreras* 2038, **C** & **D** from *Contreras* 2275, **E**, **F** & **U–W** from *Contreras* 2327, **G** from *Contreras* 2261, **H** - **Q** from *Contreras* 1850, **R** from *Contreras* 1851, **T** from *Contreras* 2372, **S** from *Hinton* 7746. Drawn by Sue Wickison.

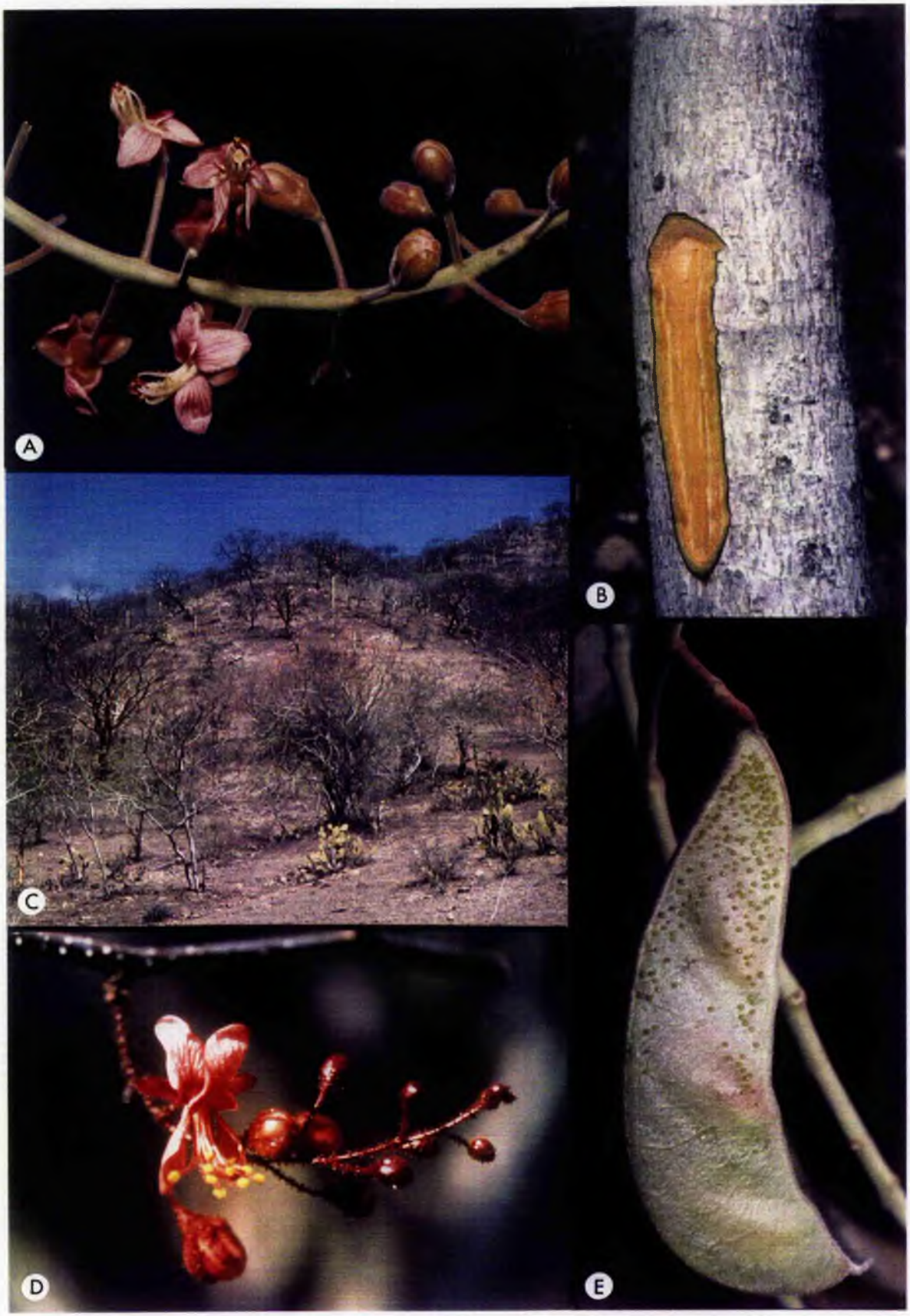


FIG. 32. *Caesalpinia hintonii*: **A** flowers; **B** bark; **C** habitat, Guerrero, Mexico; *C. melanadenia:* **D** inflorescence (*Lewis et al.* 1792, photo.: C.E. Hughes); *C. hintonii*: **E** fruit. **A-C** and **E**: *MacQueen et al.* 428.

ECOLOGY. Tropical deciduous woodland, on open rocky slopes and in wooded ravines, 150--1300 m.

PHENOLOGY. Flowering from late December to June, fruiting from late January to June

VERNACULAR NAMES. "Trompetilla", "Juancanchire".

NOTES. The *C. hintonii* group, which includes *C. epifanioi, C. laxa, C. macvaughii* and *C. melanadenia*, is confined to the Rio Balsas Depression in the Mexican states of Michoacan, Guerrero and Puebla, a zone high in endemism and with many unique legume taxa. The group would appear to be undergoing present day speciation and a detailed field study is needed to determine how many species or infraspecific taxa should be recognised. All known species in the group appear to be mainly pollinated by territorially aggressive bees in the genus *Centris* and the flower morphologies have apparently been canalized by this particular bee pollination syndrome. Within *C. hintonii*, as circumscribed here, three forms can be recognised as discussed by Contreras (1991). The comments that follow are translated from Contreras's spanish text: "Two of the forms generally have arcuate or pendulous inflorescences with long, narrow pedicels which on occasion are bent or twisted so that the flowers are resupinate. One of these two forms [e.g. *Contreras* 2327] has an indumentum of simple hairs mixed with glands; larger leaflets; larger scarlet flowers with their pedicels articulated at or a little below the calyx tube, and a legume with abundant red, stipitate pixie-cup glands, all characters corresponding to those mentioned by Sandwith (1937) in the protologue of *C. hintonii*. The other form is glabrous with glands restricted to floral structures; leaves smaller with fewer leaflets, flowers smaller with the sepals yellowish and the petals salmon pink, the pedicels articulated at or below their middle [not at or just below the calyx tube as stated by Contreras], the pod is completely glabrous and only occasionally presents stipitate glands on its surface. Both forms coexist in adjacent localities in the western part of the Rio Balsas Depression in the states of Michoacan and Guerrero in the region of Infiernillo. The third form is isolated from the other two and grows in the eastern part of the Rio Balsas Depression in Puebla and Guerrero; it is characterized by erect or ascending inflorescences, flowers non-resupinate with pedicels appressed-ascending, an abundant indumentum on inflorescence and flowers and the fruit with lime green, cupular or annular [doughnut-shaped] glands." Contreras

goes on to say that "these differences do not, for the moment, justify the recognition of distinct species and that it is necessary to study the biosystematics of the plants before any taxonomic category can be assigned to them".

On pendulous inflorescences the flower pedicels are twisted and the flowers consequently resupinate. This inversion of the flowers on a pendulous inflorescence naturally presents the flower the right way up for a visiting pollinator thus permitting all orientation cues to function normally.

The relationship between the various forms of *C. hintonii* and the closely related *C. macvaughii* and *C. laxa* need to be further investigated.

17. **Caesalpinia macvaughii** *J.L. Contr. & G.P. Lewis* in Kew Bull. 47: 309 (1992). Type: Mexico, Guerrero, Mpio. Zirándaro de Chávez, 8 March 1988, *Contreras* 2343 (holotype FCME, isotypes K!, MEXU).
Caesalpinia laxa sensu McVaugh, pro parte quoad McVaugh 22517, non Benth.

Shrub to medium-sized tree, 2--8 m tall; bark grey, pruinose, exfoliating; branchlets reddish, glabrous. *Leaves* bipinnate; stipules caducous; petiole (1--)2--6(--8.5) cm long; rhachis (0.1--)4.5--14(--16.7) cm long; pinnae in (2--)4--6(--7) opposite pairs plus a terminal pinna; leaflets in (4--)6--11 opposite pairs per pinna, oblong-elliptic, obtuse to rounded at apex, oblique at base, (5--)8--17(--19) x (2--)3--7(--8) mm, pilose when young, glabrous when mature, the margin black-gland-dotted. *Inflorescence* an axillary or terminal raceme or panicle up to 40 cm long, glabrous; bracts ovate, long-acuminate, (3.3--)4--5 x 1.6--2.4 mm, squarrose, pilose, caducous; pedicels 6--8 mm long, pilose, articulated in the lower $^1/_4$. *Calyx* red, lower sepal cucullate, 5--6.2 mm long, obtuse, ciliate, the four other sepals (4.5--)5--6 mm long. *Corolla* yellow, standard petal ovate, apex acute, base cordate, c 8--10.5 x 3.2--4.5 mm (including a 2.2--3 mm claw), upper and lower lateral petals ovate to broadly ovate, c 6--9.5 x (3--)4--6.5(--7) mm (including a 0.5--1.5 mm claw), all petals glandular-ciliate on the blade, with stipitate green glands on the claw and blade base. Stamen filaments curved, 6--9.5(--10) mm long, flattened and densely villous at the base, pilose on the basal part, green stipitate glands on upper part; anthers elliptic, 1.2--1.5 x 0.8--1.1 mm. Ovary densely pubescent, occasionally with ring-

or cup-shaped glands intermixed, stipe 0.2--0.5 mm long; style curved, (1.3--)4--6.3 mm long, pubescent on basal $^1/_2$--$^3/_4$, 2--3-ovulate. *Fruit* a maroon to reddish, falcate, subcoriaceous, elastically dehiscent pod, 3.2--4.9 x 1(--1.4) cm, pilose, occasionally with doughnut-shaped glands intermixed, valves twist after dehiscence, 1--2(--3)-seeded. *Seeds* yellowish to maroon, broadly ovate, compressed, 8--9 x 6--8 x c 0.25 mm. (Figs.33 & 34, Map 7).

DISTRIBUTION. Mexico: Michoacan and Guerrero.

MEXICO: Michoacán, Mpio. of La Huacana, c 35 km S of Nueva Italia near Infiernillo dam, 20 Jan. 1982, *Lorence et al.* 3820 (K!, MEXU); 3 km S of Nueva Italia, 24 Feb. 1965, *McVaugh* 22517 (ENCB, NY!, photo K!); **Guerrero,** Mpio. Zirándaro de Chávez, 5 km W of Guariche, 8 March 1988, *Contreras* 2343 (holotype FCME, isotypes K!, MEXU); 3 km W of Guariche, 8 March 1988, *Contreras* 2340 (FCME, K!); same locality and date, *Contreras* 2341 (FCME, K!), 21 June 1989, *Contreras* 2513 (FCME), *Contreras* 2514 (FCME); 3.5 km W of Guariche, 8 March 1988, *Contreras* 2342 (FCME, K!); 6 km W of Guariche, 21 June 1989, *Contreras* 2508 (FCME); 2 km N of Aratichanguito, 20 Sept. 1989, *Contreras* 2520 (FCME).

ECOLOGY. Tropical deciduous woodland, 180--200 m.

PHENOLOGY. Flowering and fruiting in February and March.

NOTES. *Caesalpinia macvaughii* is apparently endemic to the basin of the Ríos Balsas and Tepalcatepec. It is related to *C. hintonii* from which it differs in its red calyx, yellow corolla, most leaflets oblong-elliptic to oblong and distributed along the length of the pinnae rhachis, erect pedicels which are relatively thick and articulated close to their bases, and glands on the fruit surfaces (when present) yellowish-green, ring-discoid or cupuliform and very short stipitate. In contrast true *C. hintonii* (see notes under that species where three forms are discussed) has salmon-pink to scarlet calyces and corollas, most leaflets obovate and restricted to the distal part of the leaf rhachis (including the petiole), the pedicels patent and thin, articulated at their middle or near to the base of the calyx tube, and glands on the fruit surface (when present) wine-red in colour, cupuliform and long-stipitate.

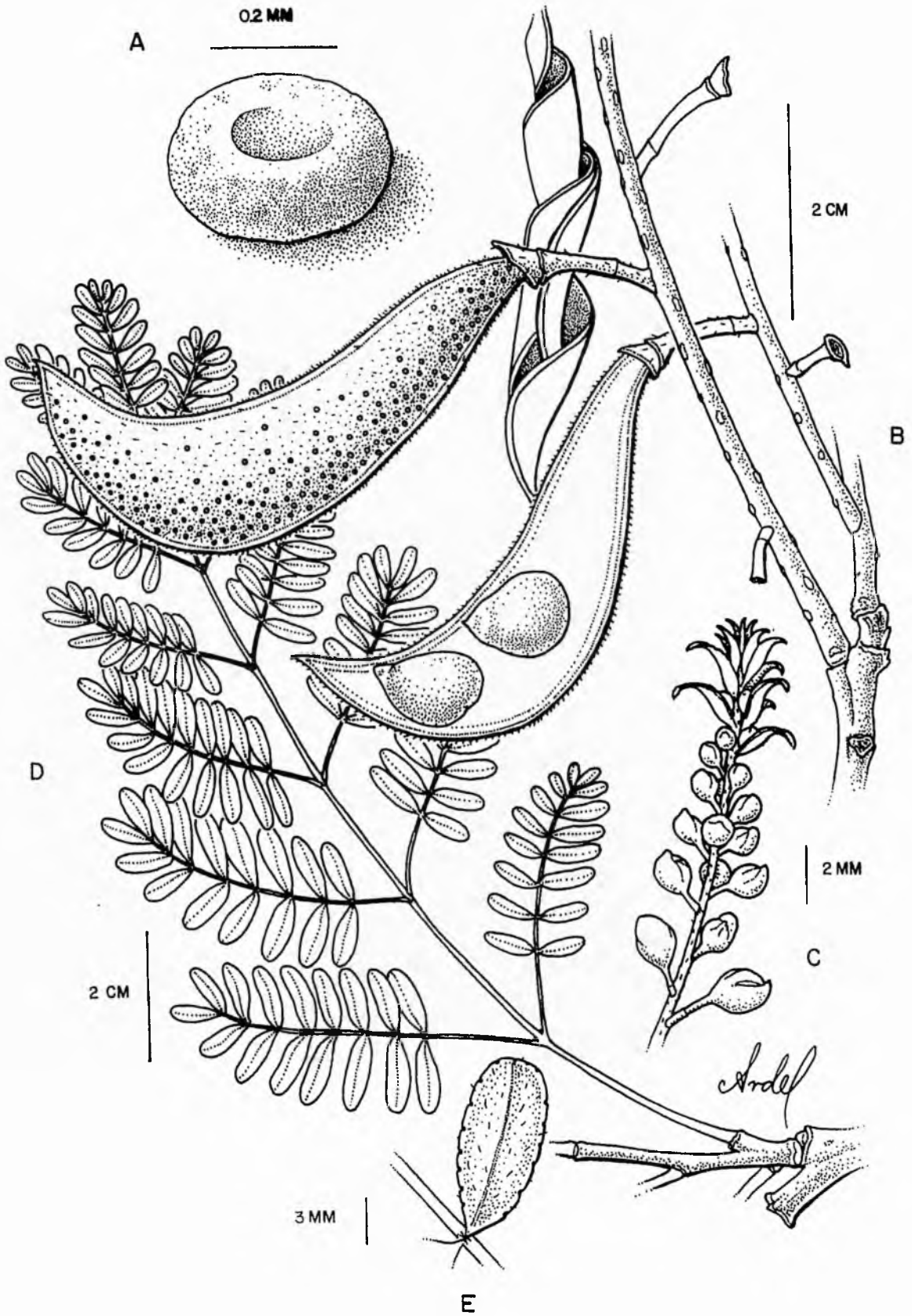


FIG. 33. *Caesalpinia macvaughii*. **A** detail of fruit gland; **B** fruits, including a twisted valve; **C** inflorescence apex showing bracts; **D** bipinnate leaf; **E** detail of leaflet. **A** & **B** from *Contreras* 2340, **C** from *Contreras* 2343, **D** & **E** from *Contreras* 2536. Drawn by Arturo Delgado.

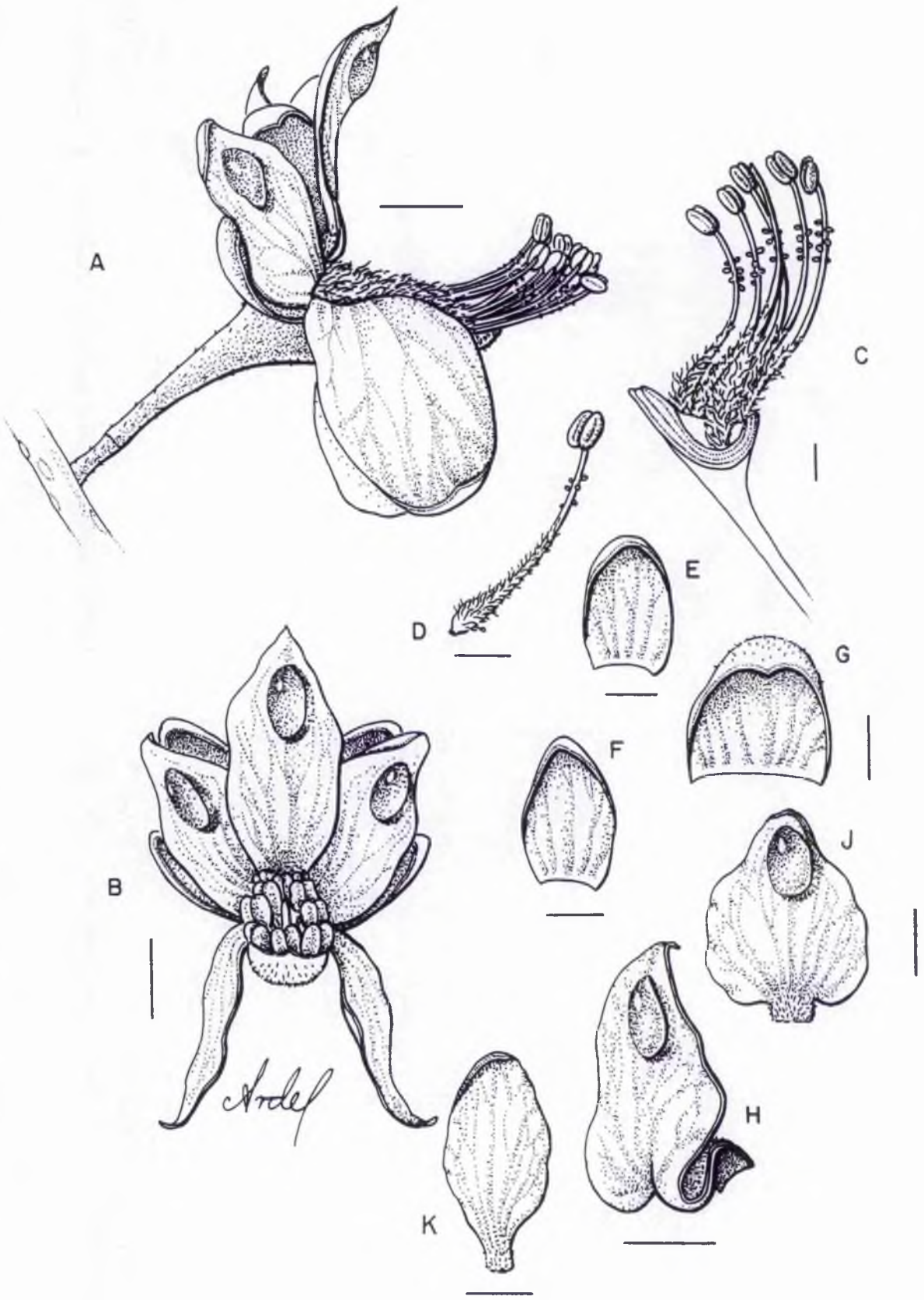


FIG. 34. *Caesalpinia macvaughii*. **A** flower, side view; **B** flower, front view; **C** stamens and gynoecium; **D** single stamen; **E** adaxial sepal; **F** lateral sepal; **G** abaxial sepal; **H** adaxial petal; **J** lateral petal; **K** abaxial petal. Scale bar equals 2 mm. All from *Contreras* 2343. Drawn by Arturo Delgado.

18. **Caesalpinia epifanioi** *J.L. Contreras* in Anales Inst. Biol. UNAM 58: 55 (1989). Type: Mexico: Guerrero, Mpio. of Mártires de Cuéllar, 18 Feb. 1986, *Contreras* 1825 (holotype FCME, isotype MEXU).

Unarmed shrub or tree, 2--4 m tall; bark grey, smooth, young branches red or yellowish. *Leaves* bipinnate; stipules broadly ovate, 1.4--2.3 mm long, densely pilose on dorsal surface, glandular fimbriate, caducous; petiole 1.9--5.7 cm long, glabrous or glandular-setose at the base; rhachis (when present) 1.3--2.2 cm long, glabrous; pinnae in 1--2 opposite pairs plus a terminal pinna; leaflets in (1--)2--3(--4) opposite pairs, oblong-ovate, obovate to orbicular, apex rounded, obcordate or truncate, base oblique, (0.5--)1--2(--2.5) x (0.4--)0.7--1.1(--1.4) cm, both surfaces glabrous, venation obscure (blade ± fleshy), occasionally glandular-punctate on the margin. *Inflorescence* a raceme, rhachis densely white pubescent; bracts ovate-acuminate, 2.7--5.5 mm long, white pubescent with stipitate glands intermixed, the margin glandular-ciliate, caducous; pediels 6.5--10(--12.5) mm long, white pubescent. Flowers of one inflorescence all or some with a short gynoecium (functionally male). *Calyx* red, lower lobe cucullate, 6.5--8(--9) mm long, the margin entire or glandular-ciliate and vesiculate, the other lobes 6--8.8 mm long, all lobes pubescent and sometimes stipitate-glandular. *Corolla* yellow or orangish, the standard petal ovate, the blade 8--10.5 x 5.8--8 mm, the claw (0.3--)0.8--1.7 mm long with a fimbriate calosity at its apex on the inner surface; upper lateral petals broadly ovate to obovate, 8--11 x 4.8--7.5 mm, apex rounded, claw 0.3--1.2 mm long; lower lateral petals obovate, 7.8--11.5 x 4.5--7 mm, apex rounded, claw 0.5--1.5 mm, all petals stipitate-glandular at the base on outer surface and the margins glandular on the basal $^1/_5$--$^1/_4$ and vesiculate on the upper $^1/_2$. Stamen filaments curved, 10--15.5 mm long, densely villous on lower $^1/_2$, stipitate-glandular in upper $^1/_2$; anthers elliptic, c 2--2.5 x 1--1.6 mm. Ovary densely pubescent and occasionally with a few glands at the base or pilose and covered in red, stipitate, pixie-cup glands; style (of hermaphrodite flowers) (c 8--)9.5--13.5 mm long, white tomentose or pilose on basal $^1/_3$--$^1/_2$, style (of functionally male flowers) 2--6.8 mm long, 2--3-ovulate. *Fruit* a falcate, subligneous, elastically dehiscent pod, 3--5.5 x 1.1--1.6(--2.2) cm, valves twist after dehiscence, pubescent with the occasional gland at the base or pilose and with brownish or purple stipitate glands over entire surface, 1--3-seeded. *Seeds* yellowish or brownish, broadly ovate, 8--12 x 7--10 x 1.5--2.5 mm.

Seedling germination phaneroepigeal, cotyledons foliaceous, persistent, first eophyll pinnate with 2--3 pairs of leaflets, second eophyll alternate, bipinnate with one pair of opposite pinnae plus a teminal one, metaphylls bipinnate with 1--2 pairs of pinnae plus a terminal pinna, hypocotyl and epicotyl white pilose and stipitate glandular. (Fig. 5N, Map 7).

DISTRIBUTION. Endemic to the state of Guerrero in Mexico.

MEXICO: Guerrero, Mpio. of Mártires de Cuéllar, 3 km E of San Francisco Ozomatlán on route to Ahuetlixpa, 18 Feb. 1986, *Contreras* 1825 (holotype FCME, isotype MEXU); 1 km E of San Francisco Ozomatlán, road to Ahuetlixpa, 2 July 1987, *Contreras* 2039, 2040, 2041, 2042, 2045 (FCME, K!); 1.5 km E of San Francisco Ozomatlán, road to Ahuetlixpa, 5 Feb. 1988, *Contreras* 2293, 2294 (FCME, K!); 6 km E of San Francisco Ozomatlán, 18 Feb. 1986, *Contreras* 1818 (FCME, K!, MEXU); 9 km E of San Francisco Ozomatlán, 7 Feb. 1985, *Ocampo & Contreras* 115 (FCME, K!, MEXU); 8 km W of San Francisco Ozomatlán, road to San Miguel Tecuixiapan, 7 Feb. 1985, *Ocampo & Contreras* 124 (FCME, K!, MEXU); 18 Feb. 1986, *Contreras* 1835 (FCME, K!, MEXU); 2 July 1987, *Contreras* 2048 (FCME, K!).

ECOLOGY. Tropical deciduous woodland, on slopes, calcareous and conglomerate soils, 500--550 m.

PHENOLOGY. Flowering and fruiting January and February.

19. **Caesalpinia melanadenia** *(Rose) Standley* in Contribs. U.S. Nat. Herb. 23: 425 (1922). Type: Mexico, Puebla, near Tehuacán, 1 Sept. 1906, *Rose* 11249 (holotype US!).

Poinciana melanadenia Rose in Contribs. U.S. Nat. Herb. 13: 303 (1911).

Poincianella melanadenia (Rose) Britton & Rose in N. Amer. Flora 23(5): 334 (1930).

Unarmed, multiple-stemmed shrub or small tree with contorted branches, 1--6.5 m tall; main stems 5--12 cm in diam.; bark of main stems pale grey almost white, smooth, with scattered ± pustular, white lenticels, young stems dark reddish-brown with white pustular lenticels, older branches almost black; outer bark slash pea-green, inner slash white; stems

sparsely pubescent to glabrous. *Leaves* bipinnate; stipules ovate, acute, 2 mm long, pubescent, stipitate-glandular, the margins fimbriate, caducous; petiole 1.8--2.5 cm long, glabrous or sparsely pubescent near base, stipitate-glandular (sometimes densely so) on basal $^1/_2$; rhachis 1.2--1.5 cm long or lacking, stalked glands present at pinnae insertions and below leaflet pulvinules; pinnae in 1--2 opposite pairs plus a terminal pinna, terminating in a red, filiform, pubescent, caducous mucro; leaflets bluish-green contrasting with the pinkish-red petiole and rhachis, in 3--4 opposite pairs, oblong-elliptic to obovate, apex acute, base asymmetric, 4--9 x 2--4 mm, both surfaces glabrous; venation obscure, only main vein evident, this terminating in a dark gland; leaflet blade eglandular or dark glands in upper $^1/_6$--$^2/_3$ of the margin, the margin then crenulate. *Inflorescence* a 10--20-flowered raceme arising from a short, woody brachyblast, glabrous, densely glandular with red, stipitate pixie-cup glands; bracts red, ovate, acute, c 2 mm long, densely stipitate-glandular, early caducous; pedicels c 7 mm long, densely stipitate-glandular, articulated c 1.5 mm below calyx. *Calyx* red, the lobes 6.5--7 mm long, lower lobe ± cucullate, margins stipitate-glandular and fimbriate. *Corolla* dark scarlet-pink; standard blade broadly triangular-hastate, 8--10 x 5 mm (including a 3 mm claw), dorsal surface of blade stipitate-glandular on basal $^1/_2$, claw and base of blade thickened, the inner surface of the claw apex with two, overlapping, crested, fin-shaped, pubescent ridges; upper lateral petals ovate-elliptic, 9--10 x 6 mm (including a 1 mm claw), basal $^1/_4$--$^1/_3$ of blade with stipitate-glandular margin, claw pubescent on inner surface, sparsely stipitate-glandular on margins; lower lateral petals narrowly obovate to obovate, 8--10 x 3.5--5 mm (including a 1.5 mm claw), base of blade with a few stipitate glands on margin, claw twisted, its outer surface sparsely to moderately pubescent and sparsely stipitate-glandular. Stamen filaments scarlet-pink, arcuate-falcate, 13--15 mm long, moderately pubescent on basal $^1/_4$--$^1/_2$, sparsely stipitate-glandular on upper $^1/_2$; anthers yellow, c 1.25 x 1 mm. Ovary pubescent and densely glandular; style arcuate, c 12 mm long; stigma a terminal, tubular, unfringed chamber. *Fruit* an elastically dehiscent, subligneous pod, 3.8--4.3 x 1.2 cm (including a 2 mm apiculate beak), moderately to densely pubescent, with dark purplish-black, stipitate pixie-cup glands scattered over valve surface, 2--3-seeded. *Seeds* ovate-suborbicular, 7 x 5--7 x 2 mm, yellowish or pale brown-ochre, shiny. *Seedling* germination phaneroepigeal, cotyledons foliaceous,orbicular, apex rounded, base cordate, persistent at least to first metaphyll, first eophyll pinnate with 3 pairs of opposite leaflets,

second eophyll alternate to first, bipinnate with one pair of opposite pinnae plus a terminal pinna, each with 3--4 pairs of opposite leaflets, hypocotyl glabrous and sparsely stipitate-glandular, epicotyl pubescent and stipitate-glandular, the pixie-cup glands with pink stalks and yellow heads. (Figs. 32D & **35**, Map 7).

DISTRIBUTION. Mexico: Puebla and just over the border into Oaxaca.

MEXICO: Puebla, road Coxcatlan to Tilapa, 13 Oct. 1968, *Boege* 999 (MEXU!); between Zapotitlán Salinas and Acatepec, 36.6 km from Tehuacán, 21 Oct. 1977, *Brenan et al.* 14373 (K!, MEXU!); Mpio. of Tehuacán, 4.4 km E of San Pablo Tepetzingo, 24 July 1979, *Chiang et al.* F-95 (MEXU!); road Tehuacán to Huajuapán de León, 6 Sept. 1979, *Chiang et al.* F-446 (MEXU!); 12 km NE of Acatepec, 16 May 1981, *Chiang et al.* F-1922 (MEXU!, TEX!); c 50 km S of Tehuacán, c 3 km N of San Jose Tilapa, 19 Feb. 1992, *Hughes et al.* 1641 (K!); 5 km NNW of Teotitlán del Camino, 22 March 1989, *Lewis et al.* 1791 (FCME!, K!, MEXU!); same locality and date, *Lewis et al.* 1792 (BR!, FCME!, FHO!, K!, MEXU!, NY!); S of Zapotitlán Salinas on highway 125, 2 km along turn off to Los Reyes Mexontla and San Luis Atolotitlan, 21 March 1989, *Lewis et al.* 1787 (K!, MEXU!); c 3 km W of Zapotitlán Salinas, 21 March 1989, *Lewis et al.* 1784 (BR!, FCME!, FHO!, K!, MEXU!, NY!); between Coxcatlan and Tilapa, 8 Nov. 1966, *Ripley & Barneby* 14723 (NY!); near Tehuacán, 1 Sept. 1906, *Rose & Rose* 11249 (holotype US!); 3 km W of San Antonio Texcala, 24 Oct. 1964, *Rzedowski* 19131 (MEXU!, TEX!); c 2 km SE of Zapotitlán Salinas, 1 Dec. 1986, *Salinas et al.* F-3748 (TEX!); c 6 km SSW of Axusco, 4 Oct. 1986, *Salinas & Solís* F-3576 (TEX!); 7 km S of Chilac, 24 Nov. 1985, *Salinas & Dorado* F-3092 (MEXU!, TEX!); 3 km SE of San Rafael, 16 Feb. 1978, *Sousa et al.* 9036 (MEXU!); 3 km SE of San Antonio Texcala, 10 Feb. 1977, *Sousa et al.* 6945 (MEXU!, TEX!); Las Ventas, c 5 km NE of Zapotitlán Salinas, 17 Oct. 1976, *Sousa et al.* 6178 (MEXU!, MO!); **Oaxaca**, Oaxaca to Tehuacán, km 150, 16 Jan. 1978, *Bamps* 6178 (BR!); road Tehuacán to Teotitlán, 16 Jan. 1978, *Téllez* 505 (MEXU!); 20 km N of Cuicatlán on road to Tecomovaca, 9 Nov. 1987, *Vásquez et al.* 4014 (NY!).

ECOLOGY. Dry semi-deciduous cactus thorn scrub, in sandy arroyos, on calcareous hard pan, 800--1960 m.

PHENOLOGY. Flowering and fruiting from October until March, the fruits sometimes persisting until May, occasionally a second flowering between July and September.

NOTES. The species is related to *C. hintonii* from the Rio Balsas Depression which has similar pinkish-red flowers.

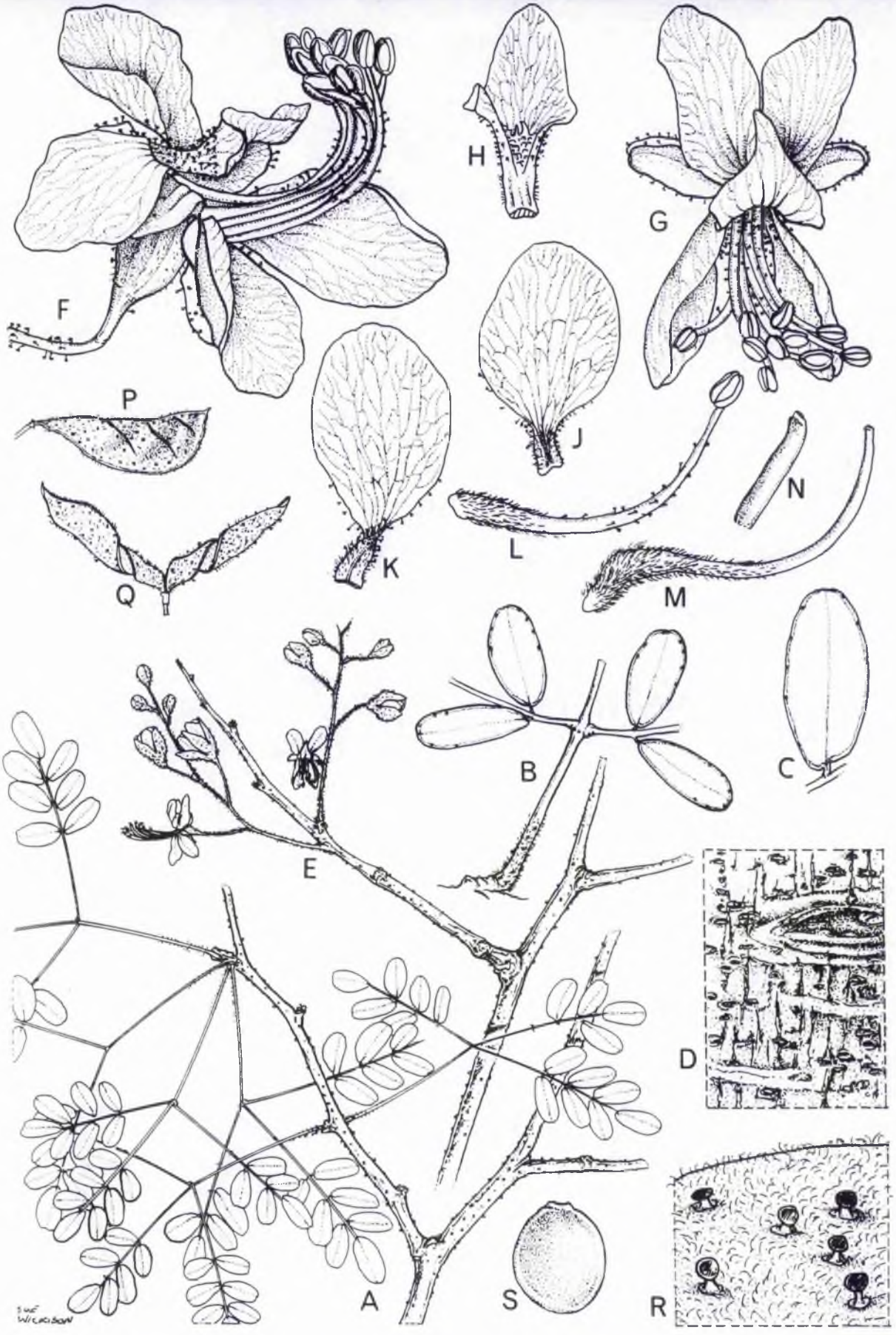


FIG. 35. *Caesalpinia melanadenia*. **A** foliage x 1; **B** petiole and basal leaflets x 4½; **C** leaflet undersurface x 6; **D** bark section x 1; **E** part inflorescence x 1; **F** flower side view x 4½; **G** flower front view x 4½; **H** standard petal x 4½; **J** upper lateral petal x 4½; **K** lower lateral petal x 4½; **L** stamen x 4½; **M** gynoecium x 4½; **N** stigma x 9; **P** fruit x 1; **Q** twisted valves of dehisced fruit x 1; **R** glands on fruit surface x 12; **S** seed x 3. **A** & **D–N** from *Lewis et al.* 1792, **B**, **C**, **P** & **S** from *Lewis et al.* 1784, **Q** from *Lewis et al.* 1791. Drawn by Sue Wickison.

20. **Caesalpinia eriostachys** *Benth.*, Bot. Voy. Sulphur : 88 (1844). Type: Costa Rica, Cocos Island, *Barclay* s.n. (lectotype K!, chosen here).

Poincianella eriostachys (Benth.) Britton & Rose, N. Amer. Fl. 23(5): 332 (1930).

Schizolobium covilleanum Pittier in Contrib. U.S. Nat. Herb. 18: 231 (1917).

Type: Panama: Prov. Coclé, between Aguadulce and Chico River, *Pittier* 5105.

Unarmed multiple-stemmed shrub to medium-sized, single-trunked tree, (1--)4--30 m tall, DBH 10--50 cm, mature trunk of larger trees intricately fluted, branching open, the crown often an inverted-cone shape; bark of older trees dark grey, vertically fissured, scaley or shaggy, bark of younger trees and main branches of older trees greyish-white or mottled various shades of grey, smooth, vertical stretch marks and horizontal dot-dash flush lenticels, upper branches sometimes horizontally ringed shades of grey; outer bark slash green, inner slash whitish or cream, cut bark with odour of garden peas with a hint of onions; young stems and leaf rhachides finely pubescent, stems, rhachides, young foliage and axillary buds usually with a dense stellate indumentum. *Leaves* bipinnate; stipules filiform, unbranched, ± falcate, c 4--5 x 0.5 mm, inner margin stellate hairy, early caducous; petiole (0.3--)1--3 cm long; rhachis 2.5--13.5 cm long; pinnae in 5--10 opposite to ± alternate pairs, usually with an additional terminal pinna but this sometimes lacking; leaflets 10--26 per pinna, alternate, sessile, oblong-rhombic (less often narrowly triangular), apex rounded to obtuse, base obliquely truncate, 5--13(--16) x 2.5--7.5(--11) mm, young flush foliage strikingly discolorous, pinkish-red above, green beneath, small reddish glands sometimes present below pulvinule on pinna rhachis, both surfaces of leaflets glabrous, (the margins sometimes ciliate) to densely white pubescent; the main vein excentric, secondary venation brochidodromous, tertiary venation reticulate; subepidermal, dark glands usually scattered over leaflet blade, most evident on lower surface, sometimes lacking, main vein often terminated by a dark gland. *Inflorescence* a 15--50-flowered axillary or terminal raceme, frequently compounded into a leafless, terminal pseudopanicle; rhachis with a rusty-brown stellate indumentum, this becoming paler with age; flowers sometimes arranged in whorls of four along rhachis; bracts ovate to lanceolate, acute, c 2.5--5 mm long, densely stellate hairy, early caducous; pedicels 6--19 mm long, articulated 4--9 mm below calyx (either above or below mid-point of pedicel).

Calyx with a dense stellate indumentum, lower lobe slightly cucullate, 7--12 mm long, margin fimbriate, pubescent, eglandular, other four lobes 6.5--11 mm long, inner surfaces densely tomentellous, all lobes with scattered subepidermal, dark, dot-dash glands (these often difficult to observe before dissection of flower due to dense stellate indumentum on outer surface of lobes). *Corolla* bright yellow; standard petal with network of orange veins, blade suborbicular, 10--12 x 8--13 mm (including a 3--4 mm claw), base of blade flapped upwards, claw thick and fleshy, a tuft of hairs at its base, stalked pixie-cup glands scattered on margins, the stalks sometimes hairy, upper lateral petals with a broadly triangular to suborbicular blade, 12--16 x 11--15 mm (including a 2--3 mm claw), the claw thick, pubescent and stipitate-glandular, lower lateral petals with suborbicular blade, 12--15 x 10--12 mm (including a 2--3 mm claw), claw stipitate-glandular, all lateral petals with scattered subepidermal dot glands in blades. Stamen filaments 10--12 mm long, pubescent on basal $^1/_3$--$^2/_3$, densely glandular with stalked-glands for entire length; anthers 1.5--2 x 0.75--1 mm, subepidermal glands sometimes visible in apices of thecae. Ovary densely tomentellous, glandular (sometimes along upper margins only) or eglandular; style pubescent and stipitate glandular, slightly swollen towards apex; stigma a terminal or subterminal fringed chamber. *Fruit* a subligneous, explosively dehiscent, scimitar-shaped pod, 7--13(--14.7) x 1.6--2.7 cm (including an apical beak up to 1 cm long), valves densely tomentellous (velvety to the touch) to glabrous, subnitid, prominently veined, twisting after dehiscence, occasionally sparse, subsessile, reddish glands on young fruits, 4--8-seeded. *Seeds* ovate, compressed pyriform, margin ± narrowly keeled, 14--16 x 10--12 x 2--3 mm, olive-fawn coloured, drying creamish-khaki. *Seedling* germination phaneroepigeal, first eophyll with two opposite to subopposite pairs of pinnae and a single terminal pinna, lateral pinnae with 15 alternate leaflets, terminal pinna with 5 opposite pairs of leaflets, second eophyll alternate to first, similar in pinnae and leaflet formula. (Figs. 9D, 11A, **36** & 37C-E, Map 9).

DISTRIBUTION. Mexico: Sinaloa, Jalisco, Colima, Michoacan, Guerrero, Oaxaca and Chiapas; Guatemala; Honduras; El Salvador; Nicaragua; Costa Rica and Panama.

MEXICO. Sinaloa, Nuevo Mundo, 26 Jan. 1940, *Gentry* 5371 (F!, MEXU!, NY!); 11 Dec. 1942, *Gentry* 6782 (NY!); Culiacan, 24 Feb. 1940, *Gentry* 5717 (MEXU!, NY!); 40 km S of Culiacan on road to

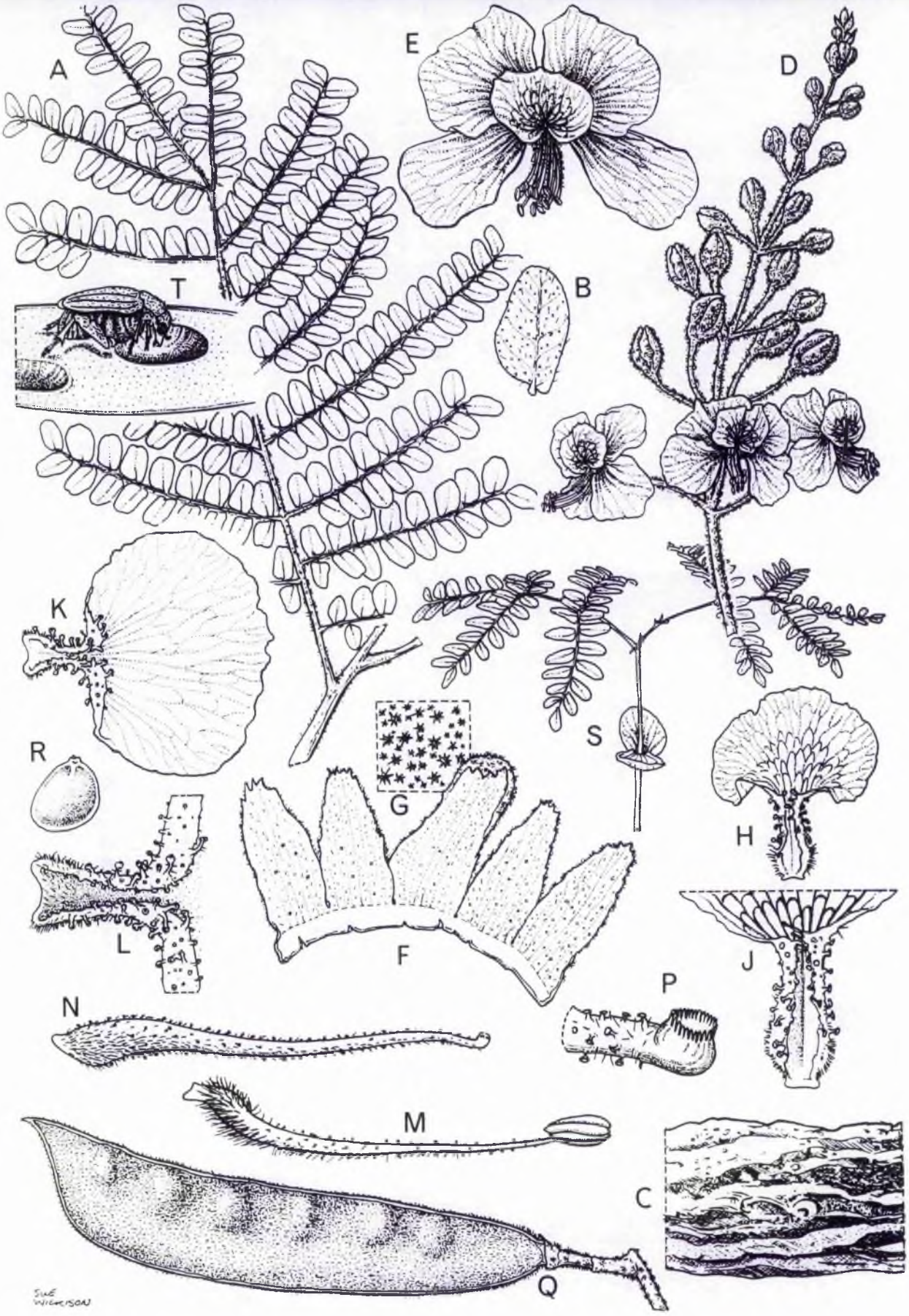


FIG. 36. *Caesalpinia eriostachys*. **A** part bipinnate leaf x 1; **B** median leaflet undersurface x 3; **C** bark section x 1½; **D** inflorescence x 1; **E** flower x 1; **F** calyx opened out x 3; **G** detail of stellate hairs on calyx x 18; **H** standard petal x 3; **J** detail of standard petal claw x 6; **K** upper lateral petal x 3; **L** detail of lateral petal claw x 6; **M** stamen x 6; **N** gynoecium x 6; **P** stigma x 18; **Q** fruit x 1; **R** seed x 1; **S** seedling x 1; **T** bruchid emerged from seed x 9. **A**, **B** & **R–T** from *Lewis & Hughes* 1799, **C** from *Lewis et al.* 1719, **D–N** from *Lewis et al.* 1718, **Q** from *Lewis & Hughes* 1775. Drawn by Sue Wickison.

FIG. 37. *Caesalpinia gaumeri*: **A** flowers (*Lewis & Hughes* 1762); **B** inflorescences (*Lewis & Hughes* 1762); *C. eriostachys*: **C** flowers (*Hughes* 329); **D** bark (*MacQueen et al.* 408); **E** flowers and buds (*MacQueen et al.* 408). Photographs **A-C**: C.E. Hughes.

Mazatlán, 14 March 1985, *Hughes* 601 (K!, MEXU!); 7 miles S of Guamuchil, 14 Jan. 1966, *Kimnach & Lyons* 668 (MEXU!); Villa Union, Jan. 1893, *Lamb* 383 (E!, NY!); Mazatlán, El Quelite, Las Zapotes, 1910, *Ortega* 5222 (K!); Concordia, Agua Caliente, without date, *Ortega* 864 (MEXU!); Mazatlán, without date, *Ortega* 5677 (K!); Elota, La Cruz, without date, *Ortega* 47 (MEXU!); Villa Union, *Ortega* 4406 (US!); Mazatlán, March 1931, *Ortega* 6773 (BR!, F!); San Ignacio, May 1921, *Ortega* 117 (K!, US!); near Rosario, 14 April 1910, *Rose et al.* 14538a (NY!, US!); **Jalisco**, Melaque, N of Manzanillo, 24 May 1970, *Boege* 1395 (MEXU!); La Huerta, Est. Biol. Chamela, 5 March 1983, *Bullock* 1307 (MEXU!); 9 March 1982, *Bullock* 1096 (MEXU!); Est. Biol. road to Nacastilla, 3 Feb. 1977, *Magallanes* 489 (LL!, MEXU!); La Huerta, Est. Biol. Chamela, 20 Feb. 1977, *Magallanes* 514 (MEXU!); 6 April 1977, *Magallanes* 608 (MEXU!); 10 Aug. 1977, *Magallanes* 762 (MEXU!); 8 km NW of Navidad, 11--12 Dec. 1959, *McVaugh & Koetz* 1689 (MEXU!); 20--25 km S of Jilotlán, 9--10 March 1965, *McVaugh* 22886 (NY!); 6--8 km S of Tomatlán, 13 Dec. 1970, *McVaugh* 25336 (NY!); Est. Biol. Chamela, 12 Feb. 1974, *Pérez* 826 (MEXU!, NY!); La Huerta, 7 km N of Chamela, 19 Jan. 1974, *Peréz* 821 (MEXU!); Est. Biol. Chamela, without date, *Saldaña* 22 (MEXU!); **Colima**, Manzanillo, 2--18 March 1891, *Palmer* 'A' (GH!, K!); 17--18 km SSW of Colima on Manzanillo road, 13 March 1965, *McVaugh* 22974 (NY!); 27--28 Feb. 1891, *Palmer* 1309 (K!); **Michoacan**, Dist. Coalcoman, Dec. 1941, *Hinton et al.* 16216 (K!); 30 km SW of Apatzingán, 7 March 1965, *McVaugh* 22870 (MEXU!, NY!); near Tepalcatepec, 15 Nov. 1949, *Moore et al.* 5768 (GH!); Comburiadio, Mpio. of Huetamo, 25 Dec. 1977, *Núñez & Andrade* 533 (MEXU!, NY!); 9 km NW of Moroata, Mpio. of Aquila, 28 Dec. 1981, *Núñez & Soto* 3774 (MEXU!); road San Jerónimo to Churumuco, 8 Oct. 1981, *Núñez* 3234 (MEXU!); 1 km NE of Zirándaro, 9 April 1977, *Soto et al.* 89 (MEXU!); Ciriancito, 3 km N of Los Ranchos, 20 July 1979, *Sousa et al.* 10732 (MEXU!); 7 km W of Santiago, Mpio. Huetamo, 11 Feb. 1983, *Tenorio et al.* 3271 (K!, MEXU!); **Guerrero**, 2 miles E of Acapulco, 1 Jan. 1944, *Barkley* 14051 (MEXU! TEX!); nr. Acapulco, 18 Jan. 1955, *Carlson* 3064 (US!); 15 miles NW of Acapulco, 21 Jan. 1955, *Carlson* 3092 (F!, GH!, MEXU!); Puerto Marqués, Mpio. of Acapulco, 20 May 1979, *Chiang et al.* 747 (MEXU!); 2.5 km W of Puerto Marqués, 20 May 1979, *Forment* 705 (MEXU!); La Poza, Mpio. Acapulco, 18 Nov. 1981, *Lopéz-Forment* 1348 (MEXU!); km 338 road Playa Azul to Morelia, 21 May 1977, *Germán* 385 (MEXU!); 12 km from Zihuatanejo, route to Ixtla, 2 Feb. 1977, *Germán et al.* 261 (MEXU!); Acapulco, 28 May 1978, *Halbinger* s.n. (MEXU!); Coyuca, 20 Feb. 1934, *Hinton* 5659 (F!, K!, MEXU!); Jaripo, Coyuca, 5 Nov. 1934, *Hinton et al.* 6929 (K!); San Felipe, 9 Dec. 1898, *Langlassé* 709 (F!, K!, US!); 10 km SW of San Antonio, 14 Feb. 1992, *MacQueen & Nileshwar* 449 (EAP, FHO, K!, MEXU); 35 km W of Acapulco, road Tierra Colorado to Zihuatanejo, 11 Feb. 1992, *MacQueen & Nileshwar* 436 (EAP, FHO, K!, MEXU); 19 km W of San Marcos, *MacQueen et al.* 408 (EAP!, FHO!, K!, MEXU!); Acapulco, 1948, *Miranda* 4756 (MEXU!); road to Coyuca, after Pie de la Cuesta, 20 March 1948, *Miranda* 4326 (MEXU!); 2 km NE of Coyuquilla, Mpio. Petatlán, 3 Feb. 1986, *Núñez et al.* 12095 (K!); 14 km NE of La Saliterra, 8 Feb. 1986, *Núñez et al.* 12395 (K!); Acapulco, Oct. 1894-March 1895, *Palmer* 546 (E!, F!, GH!, K!); 11 km N of San Marcos, 31 Jan. 1983, *Tenorio et al.* 3143 (K!, MEXU!); 17 km NE of Zihuatanejo, 21 May 1982, *Tenorio et al.* 396 (MEXU!); 15 km NE of Zihuatanejo, *Tenorio et al.* 386 (MBM!, MEXU!); **Oaxaca**, 26 Dec. 1944, *Alexander* 169 (NY!); Tehuantepec, 15 Dec. 1944, *Alexander* 70

(F!, NY!);4 km N of Tehuantepec, 20 Feb. 1963, *Barr* 63--47 (MEXU!); Puerto Angel, 25 Dec. 1974, *Boege* 3320 (MEXU!); road Tehuantepec to Niltepec, 23 Dec. 1968, *Boege* 1057 (MEXU!); NE of Juchitán, road to San Dionicio del Mar, 25 Feb. 1981, *Cedillo* 572 (MEXU!); San Isidro Llano Grande, 26 March 1989, *Lewis & Hughes* 1799 (BR!, FHO!, K!, MEXU!, NY!); Tehuantepec, Dec. 1965, *MacDougall* s.n. (MEXU!, NY!); Dec. 1966, *MacDougall* 82 (NY!); 7 km SW of Magdalena Tequisistlan, 29 Nov. 1991, *MacQueen* 289 (EAP, FHO, K!, MEXU); 2--10 km N of Puerto Escondido, 13 Feb. 1965, *McVaugh* 22448 (MEXU!, NY!); Tehuantepec, 18 Jan. 1951, *Mejorada* 535 (MEXU!); San Geronimo, 4 April 1930, *Mell* 634 (F!, NY!); Puente Marilu, 29 Dec. 1950, *Miranda* 6806 (MEXU!); Arroyo del Chile, near Tehuantepec, Nov. 1958, *Rita* 364 (MEXU!); between Tequisistlan and Jalapa, 9 Jan. 1896, *Seler & Seler* 1675 (K!, MEXU!, NY!); Zipolite, 7 Feb. 1976, *Shapiro* 338 (MEXU!); 5 km W of Niltepec, 21 Feb. 1978, *Sousa et al.* 9158 (MO!); 31 km E of Puerto Escondido, 13 Feb. 1976, *Sousa et al.* 5320 (MEXU!, US!); 12 km NNW of Tehuantepec, 17 March 1981, *Sousa et al.* 11941 (K!, MEXU!); 9 km NE of Barra de Santa Elena, 25 June 1977, *Sousa et al.* 7614 (MEXU!); 3 km NW of Puerto Escondido, 11 Feb. 1976, *Sousa et al.* 5285 (MEXU!, US!); 3 km W of Niltepec, 18 June 1977, *Sousa et al.* 7412 (MEXU!); 13 km WNW of Tehuantepec, 20 June 1977, *Sousa et al.* 7474 (MEXU!); 2 km E of Cazadero, 16 June 1977, *Sousa et al.* 7365 (MEXU!); Barra de Colotepec, 5 km E of Puerto Escondido, *Sousa et al.* 7096 (MEXU!); 12 km SW of La Reforma, 20 June 1977, *Sousa et al.* 7506 (MEXU!); Cipolite, W of Puerto Angel, 21 April 1976, *Sousa et al.* 5580 (MEXU!); 22 km SW of Morro, 27 Oct. 1977, *Sousa & Téllez* 8673 (MEXU!); 3 km W of Tehuantepec, 14 Dec. 1978, *Sousa et al.* 10089 (MEXU!); Morro de Mazatan, Mpio. of Tehuantepec, 20 Feb. 1978, *Sousa* 9131 (MEXU!); 3 km W of Marilu, 19 Feb. 1978, *Sousa* 9089 (MEXU!); 5 km W of Niltepec, 27 Oct. 1976, *Sousa et al.* 6617 (MEXU!); La Pita, 3 km WNW of Puerto Escondido, 21 Oct. 1976, *Sousa et al.* 6379 (MEXU!); Puerto Escondido, 20 March 1983, *Tenorio et al.* 3574 (MEXU!); 8 km E of Pinotepa Nacional, 6 April 1982, *Tenorio & Torres* 208 (MEXU!); SE of Flautas, km 199 on road Oaxaca to Tehuantepec, 12 Dec. 1985 *Torres et al.* 7869 (MEXU!); 4.9 km N of La Concepción, 20 March 1984, *Torres & Martínez* 4804 (K!, MEXU!); road from Cazadero to San Dionicio del Mar, 25 Feb. 1981, *Trigos* 572 (MEXU!, NY!); km 5 on road to Giengola & Las Pilas, 13 Dec. 1980, *Trigos & Lorence* 543 (MEXU!, NY!); Tehuantepec, 28 June 1937, *Williams* 9755 (F!); **Chiapas**, road Tuxtla Gutiérrez to Presa de la Angostura, 1 km after junction at Narisco, 13 Feb. 1985, *Hughes* 529 (K!, MEXU!); c 25 km SE of Tuxtla Gutiérrez, c 2 km NW of Acala, 9 March 1989, *Lewis & Hughes* 1775 (BR!, FHO!, K!, MEXU!, NY!); same locality, 9 March 1989, *Lewis & Hughes* 1774 (BR!, FHO!, K!, MEXU!, NY!); Jericó, SE of Tuxtla Gutiérrez, 18 Feb. 1951, *Miranda* 6903 (MEXU!); c 1.75 km NE of San Caralampio, Jan.-May 1977, *Voorhies & Sanchez* 22--2 (MEXU!); **GUATEMALA**, 20 km E of Chiquimulilla, 4 Feb. 1984, *Hughes* 406 (K!, MEXU!); c 10 km E of Rio Honda, NW of Zacapa,28 Feb. 1989, *Lewis & Hughes* 1754 (BR!, FHO!, K!, MEXU!, NY!); **HONDURAS**, 10 km E of Amarillo, 25 Jan. 1956, *Cox & Guzmán* 1168 (EAP!); c 15 km NE of Choluteca, near village of El Pillado, 2 April 1984, *Hughes* 448 (K!, MEXU!); Dept. Valle, Goascorán, 21 Jan. 1956, *Molina* 5907 (EAP!); *Molina* 5901 (EAP!, F!); Dep. Fco. Morazán, near Reitoca village, 21 Feb. 1971, *Molina* 25928 (EAP!, F!, NY!); Dep. Morazán, between Cuesta Moramulca and Sabana Grande, 22 March 1958, *Molina* 8647 (EAP!, F!); Dep. Choluteca, 3 km E of Las

Hormigas, 3 July 1974, *Repulski* 417 (EAP!); Dep. Valle, near Jicaro Galán, 11 Jan. 1949, *Williams & Molina* 15005 (EAP!); **EL SALVADOR**, W of La Libertad, 28 Jan. 1959, *Allen* 7199 (EAP!, LL!, NY!); La Union, 23 March 1939, *Beetle* 26254 (K!, US!); Dep. San Miguel, hacienda San Antonio, 1924, *Calderón* 2132 (NY!); Dep. Morazán, Jocoro, 1924, *Calderón* 2033 (GH!, NY!, US!); Dept. Libertad, Finca Santa Emilia, 11 Feb. 1946, *Carlson* 558 (EAP!, F!); San Salvador, port of Acajutla, 11 Jan. 1862, *Hayn* 459 (K!); Dept. Santa Ana, c 4 km S of San Geronimo on road to Metapan, 22 Feb. 1989, *Lewis et al.* 1747 (FHO!, K!, LAGU!, MEXU!, NY!); c 8 km W of Acajutla, 16 Feb. 1989, *Lewis et al.* 1718 (BR!, FHO!, K!, LAGU!, MEXU!, NY!, US!); same locality and date, *Lewis et al.* 1719 (BR!, FHO!, K!, LAGU!, MEXU!, NY!, US!); Dept. Sonsonate, near Acajutla, 20 March 1922, *Standley* 21979 (F!, GH!, NY!); near La Union, 13--21 Feb. 1922, *Standley* 20651 (NY!); Dept. Morazán, road San Miguel to Divisadero, 15 Dec. 1941, *Tucker* 551 (F!, LL!); c 0.1--0.8 km NW of hacienda Porrero Santo, 2 Feb. 1942, *Tucker* 880 (F!, K!, US!); San Salvador, without date, *Wendland* s.n. (K!); **NICARAGUA**, Dept. Leon, Volcán Momotombo, 29 Jan. 1980, *Araquistain & Moreno* 1088 (MEXU!); near village of El Cruce de la India on road Sebaco to Telica, 22 March 1983, *Hughes* 329 (K!, MEXU!); NE of Lago de Managua on road to San Francisco del Carnicero, 3 March 1982, *Hughes & Styles* 66 (K!, MEXU!); Prov. Segovia, Jan. 1848, *Oersted* 5061 (F!); Dept. Leon, along Rio Sinecapa, 15 Sept. 1977, *Stevens* 3860 (MEXU!, NY!); Dept. Managua 1.5--3.5 km N of Las Maderas, 26 Dec. 1978, *Stevens* 11285 (MEXU!, TEX!); Dept. Leon, near Los Brasiles, 19 March 1984, *Stevens* 22879 (NY!, TEX!); Dept. Managua, c 8.7 km E of San Benito, 4 Feb. 1984, *Stevens* 22839 (NY!, TEX!); **COSTA RICA**, Prov. Puntarenas, c 28.2 km SE of Brijo, 17 March 1978, *Almeda et al.* 4267 (MEXU!, NY!); Culebra, 26 March 1838, *Barclay* 2175 (BM!; US!); Cocos Island, without date, *Barclay* s.n. (lectotype K!); towards Cañas, 29 May 1932, *Bunk* 15606 (F!); Nicoya Peninsula, 28 Dec. 1966, *Burger & Ramirez* 4071 (F!, NY!); Nicoya, Jan. 1900, *Conduz* 13797 (GH!, K!, NY!); near Cañas, 21 Jan. 1970, *Daubenmire* 533 (F!); same locality, 31 March 1970, *Daubenmire* 675 (F!); road to Manzanillo, 6 Dec. 1968, *Davidse & Pohl* 1386 (NY!); Prov. Guanacaste, 1972, *Dawe* 73--0605A (F!); c 3 miles S of Nicoya, 25 May 1943, *Dayton & Barbour* 3098 (F!); Nicoya, 1842, *Hinds* s.n. (K!); 10 km N of Liberia, 22 Feb. 1982, *Hughes & Styles* 43 (MEXU!); 10 km W of Liberia, 23 Feb. 1982, *Hughes & Styles* 53 (K!, MEXU!); Comunidad, Carrillo, 20 March 1963, *Jiménez* 482 (EAP!, F!); San José, Morro Hermoso, Liberia, April 1966, *Jiménez* s.n. (F!, NY!); Golfo de Nicoya, Isla Chira, 8 Feb. 1984, *Khan et al.* 871 (MEXU!); Hojaucha de Nicoya, 29 Jan. 1942, *León* 955 (F!); Sardinal, 5 March 1951, *León* 3134 (EAP!); near Rio Lagarotes, 16 Feb. 1957, *Schubert et al.* 1380 (A!); Ahogados, 26 Jan. 1983, *Sousa et al.* 12701 (K!, MEXU!); between Guayabo and Salitral, 4 Feb. 1976, *Utley* 4004 (NY!, US!); Corralillo, 14 Sept. 1984, *Wiemann* 125 (LSU!); c 20--30 km W of Liberia,2 Jan. 1964, *Williams et al.* 26500 (EAP!, F!); **PANAMA**, Prov. of Coclé, valley of upper Rio Mata Ahogado, 31 Dec. 1936, *Allen* 131 (F!); near Aguadulce, 23 Jan. 1947, *Allen* 4032 (EAP!, NY!, US!); San José Island, 14 July 1945, *Erlanson* 462 (US!), same locality, 28 March1945, *Johnston* 565 (GH!); Prov. Coclé, between Aguadulce and Chico River, 7--9 Dec. 1911, *Pittier* 5105 (F, photo!); Prov. Panama, between Las Sabanas and Matias, 21 Jan. 1924, *Standley* 31901 (US!).

ECOLOGY. Low to medium stature deciduous forest, dry thorn scrub, dry savanna, low coastal hills, rocky slopes and ravines on sand, limestone, gypsum, slate and basalt, 5--700 (--1300) m.

PHENOLOGY. Flowering late October to June, fruiting December to July, the fruits sometimes persisting to November.

VERNACULAR NAMES. "Casa iguana", "Iguanero", "Iguano", "Gumago", "Hediondilla" (Mexico); "Zorro" (Honduras); "Iguana", "Pintadillo" (El Salvador); "Cuayancuavo", "Pintadillo" (Nicaragua); "Zahino", "Saena" (Costa Rica).

NOTES. "Seeds are said to paralyse animals that eat them" (*Calderón* 2033, El Salvador). Hughes (pers. comm.) has suffered violent vomiting and severe stomach cramps as a result of eating an unripe seed of the species. Urgent medical attention was needed to combat the symptoms. Larger trees are reported to furnish a hard timber (*Dayton & Barbour* 3098) and planted specimens sometimes form a living fence line.

C. eriostachys is the widest ranging species in Mexico and Central America, extending from Sinaloa in western Mexico, southwards to Chiapas and on through countries of Central America as far south as Panama. The most robust specimens with lush foliage and long racemes grow in Costa Rica. The species is taxonomically and phytochemically isolated within the Central American *Poincianella* group, principally by its differing seedling morphology (first eophyll bipinnate with alternate leaflets) dense stellate indumentum on the inflorescence and lack of 4-methylglutamic acid in the seeds.

It is not known from South America but it would seem to be quite closely related to *C. pluviosa* var. *peltophoroides* from Brazil with which it shares several similar morphological characters, including the presence of subepidermal, mucilage-filled idioblasts in pedicels, petal blades and the apices of anthers. The young foliage of both species flush a pink colour.

The species is recorded from Cuba (N. Amer. Flora 23(5): 332 [1930]) but I have seen no material to confirm its presence there.

Bentham (1844) cited "Nicoya and Cocos Island" as the localities of his new species and three herbarium sheets at K, all from Costa Rica, represent the two areas cited, namely two *Barclay* s.n. specimens from Cocos Island and a *Hinds* s.n. collection from Nicoya. McVaugh (1987) cites "Nicoya and Cocos Island" as syntypes without further comment. Contreras (1991) gives the type of *C. eriostachys* as "COSTA RICA: entre

Nicoya e Isla de Cocos, *Barclay et Hinds* s.n. (Holotipo BM)" but this is an error as it includes two distinct elements. In addition, the only specimen I could trace at BM which resulted from the voyage of the HMS Sulphur is *G.W. Barclay* 2175 collected on 26 March 1838 at Culebra, Costa Rica and this specimen was not cited by Bentham in his protologue of *C. eriostachys*.

I have chosen one of the *Barclay* s.n. specimens from Cocos Island as the lectotype of *C. eriostachys* as the specimen better fits the protologue which includes the description of foliage which is not present on the Hinds collection from Nicoya.

21. **Caesalpinia gaumeri** *Greenman* in Publ. Field Mus. Nat. Hist. Bot. 2: 330 (1912). Type: Mexico, Yucatan, Progresso, 5 March 1899, *Millspaugh* 1675 (holotype F, n.v.).

Poincianella gaumeri (Greenman) Britton & Rose in N. Amer. Fl. 23(5): 333 (1930).

Poincianella guanensis Britton in N. Amer. Fl. 23(5): 333 (1930). Type: Cuba, Remates de Guane, Pinar del Rio, April 1926, *Fors* 3965 (holotype NY!).

Caesalpinia guanensis (Britton) León in Contribs. Ocas. Mus. Hist. Nat. Col. 'de la Salle', Habana 9: 12 (1950).

Unarmed single or multiple-stemmed shrub or tree, (1.2--)4--20 m tall, main trunks 5--15 cm in diam., crown open, little-branched; bark grey, smooth, vertically shallowly fissured, lenticellate or not, outer bark slash yellowish-cream with green markings, inner slash creamish, heartwood black, hard; young stems and dormant, rounded, axillary buds glabrous or pubescent. *Leaves* bipinnate; stipules petaliferous, spathulate-cucullate, 10--12 mm long, tapering to a narrow claw, the blade streaked and dotted with dark, subepidermal glands, early caducous; petiole 1.2--3.8 cm long, pubescent, glabrescent; rhachis 3--9 cm long, pubescent or hairs along upper edge only to glabrous; pinnae in (2--) 3--4 subopposite to alternate pairs plus one terminal pinna (rarely reduced to a single pair of pinnae); leaflets alternate, 7--13 per pinna, subcoriaceous, discolorous, darker and glossy above, increasing in size towards distal end of rhachis, the terminals ovate-rhombic, 1.3--3.2(--4) x 0.6--1.9(--2.8) cm, the median leaflets ovate-rhombic to obliquely

subquadrate or subrectangular, 1.2--2.9(--4.4) x 0.7--2(--2.6) cm, apices obtuse to retuse, base inequilaterally truncate, both surfaces glabrous, the margin sometimes ciliate, secondary venation brochidodromous, tertiary venation reticulate, main vein terminating in a dark gland; dark reddish-black, subepidermal glands scattered over leaflet blade, most evident on lower surface and on young leaflets, sometimes most dense along leaflet margin. *Inflorescence* an axillary or pseudolateral 30--75-flowered raceme, after leaf fall the inflorescence appears as a large showy panicle; rhachis glabrous or very sparsely pubescent; bracts narrowly obovate-spathulate, 2 x 1 mm, the margin glandular, the blade with scattered subepidermal glands, early caducous; pedicels 8--14 mm long, articulated 2.5--6 mm below calyx, portion above articulation pubescent and glandular, below sparsely pubescent, glabrescent. *Calyx* lobes 5--6 mm long, lower lobe cucullate-imbricate, all lobes tomentulose or finely pubescent on both surfaces or outer surface glabrescent except for zone of imbrication which is pubescent, subepidermal dash and dot glands present. *Corolla* canary or golden yellow, the standard spotted or network-veined orange, blade suborbicular, 9--11 x 5--7(--10) mm (including a 3--4 mm claw) blade eglandular or with a few subepidermal glands, folded base of blade runs into inrolled, thickened claw, claw densely pubescent on margins and at base, densely glandular with short-stalked glands, upper lateral petals with obovate to suborbicular blade, 9--12(--15) x 5--8(--14) mm (including a 2--3 mm claw), lower lateral petals with a narrowly obovate blade, 10--12(--15) x 4--6(--11) mm (including a 2.5--3 mm claw), claws of all lateral petals orangish, inrolled, densely glandular with short-stalked glands, outer surface of blades with stalked glands on lower $^1/_3$--$^1/_2$, subepidermal glands present but sometimes sparse and only in upper $^1/_2$ of blade. Stamen filaments 7--12 mm long, lower $^1/_2$--$^2/_3$ pubescent, entire length glandular with sessile or short-stalked glands; anthers 1--1.5 x 0.75--1 mm. Ovary pubescent, 6-ovulate; style c 6 mm long, pubescent and glandular for entire length; stigma a fringed chamber, subterminal due to curvature of bulbous style apex. *Fruit* a dehiscent, woody pod, 6.7--10 x 2.2 cm (the width apparently consistent), valves glabrous, the thickened margin finely pubescent, 3--6-seeded. *Seeds* elliptic to ovate, 9--13 x 6--11 x 2.5 mm, yellowish or brownish-ochre, shiny. (Figs. 5Q, 37A & B & **38**, Map 13).

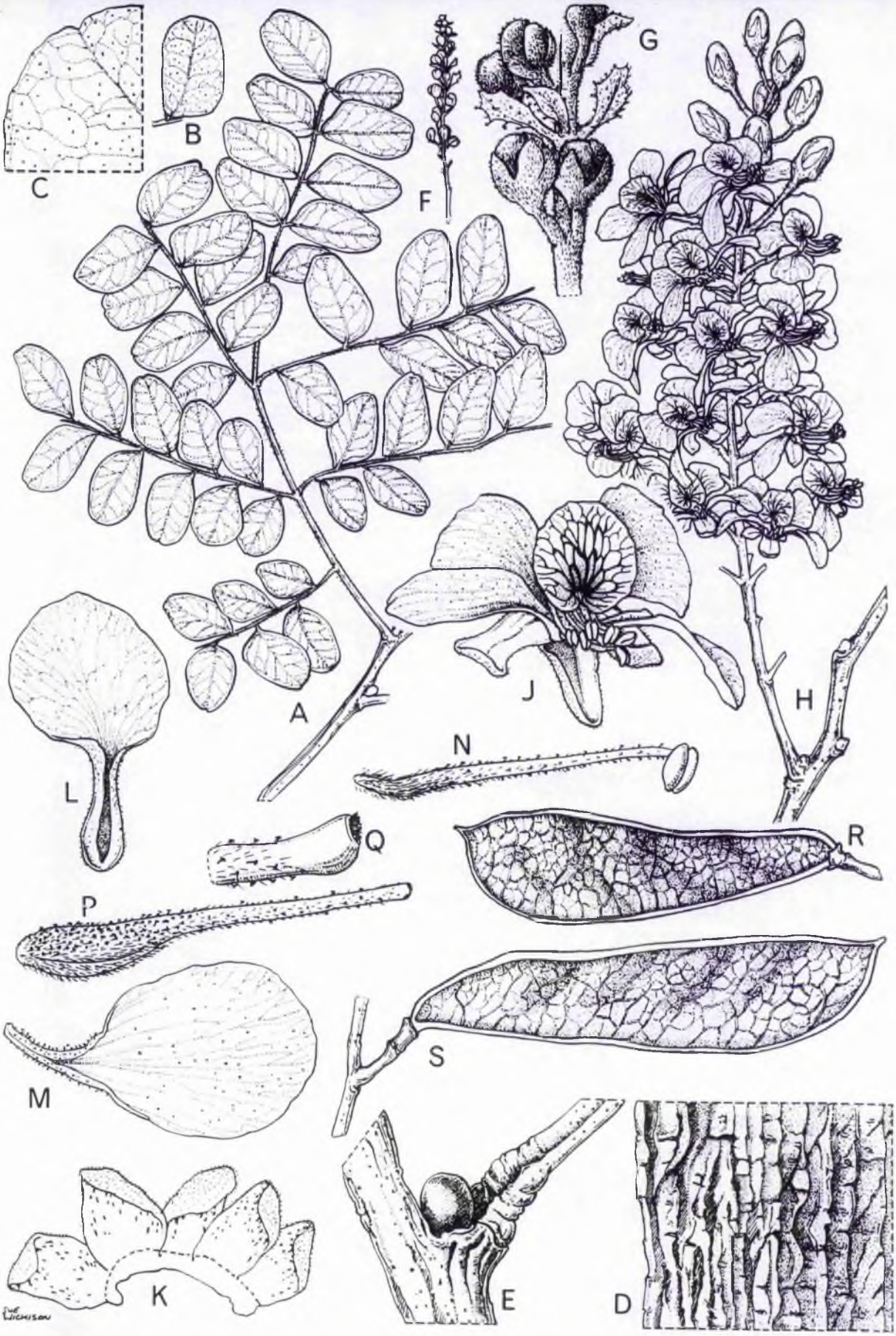
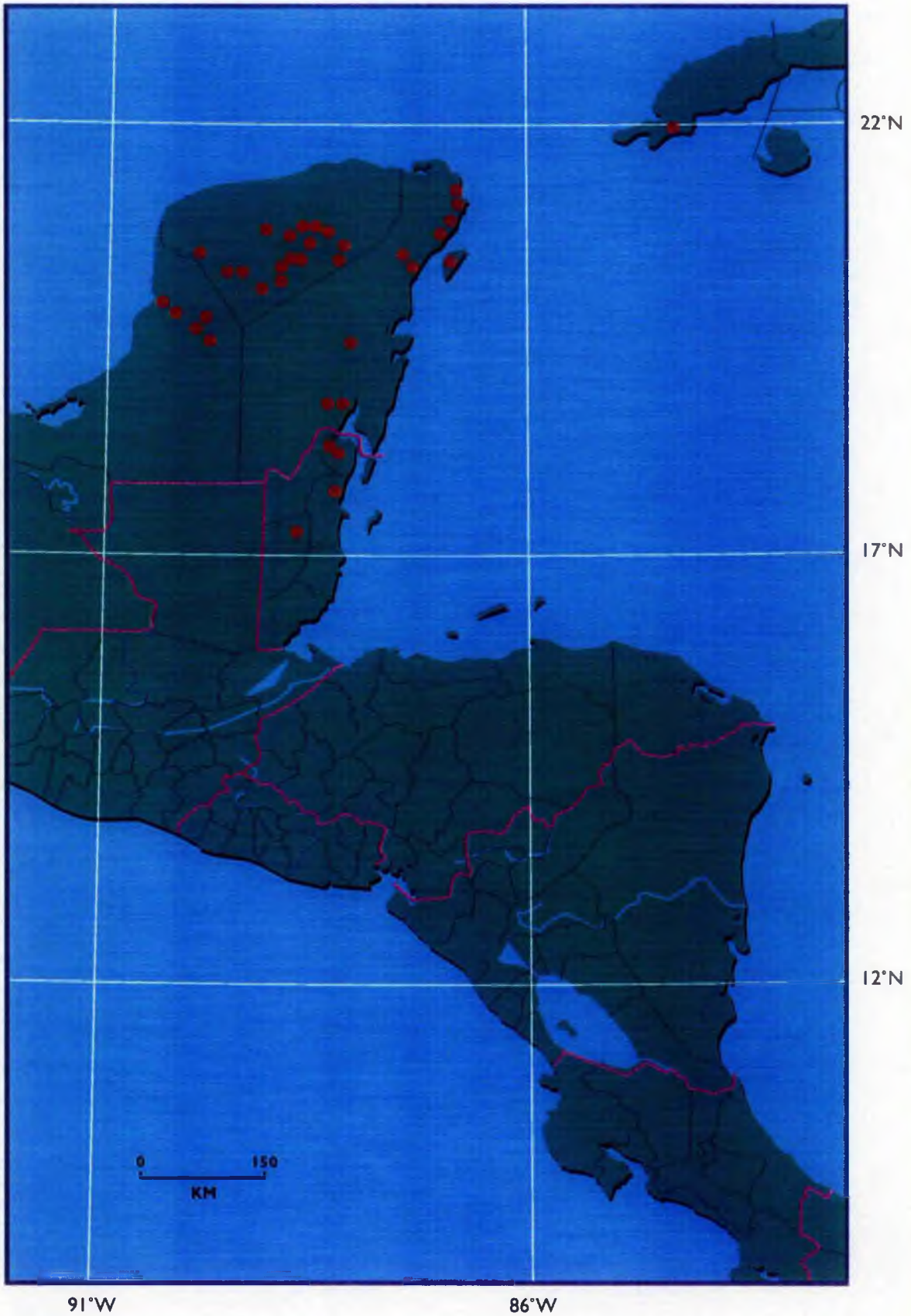


FIG. 38. *Caesalpinia gaumeri*. **A** bipinnate leaf x 1; **B** median leaflet undersurface x 1; **C** median leaflet undersurface section x 6; **D** bark section x 1½; **E** bud in axis of leaf petiole x 4½; **F** young inflorescence apex showing bracts x 1; **G** detail of inflorescence tip and bracts x 6; **H** inflorescence x 1; **J** flower x 3; **K** calyx opened out x 3; **L** standard petal x 4½; **M** lateral petal x 4½; **N** stamen x 6; **P** gynoecium x 6; **Q** stigma x 18; **R** & **S** fruits x 1. **A** from *Hughes* 492; **B–E** & **H** from *Lewis & Hughes* 1762; **F**, **G** & **J–Q** from *Lewis & Hughes* 1764, **R** & **S** from *Davidse & Brant* 32646. Drawn by Sue Wickison.

Distribution of *Caesalpinia gaumeri* (●) in the Yucatan Peninsula and Cuba



DISTRIBUTION. Belize, Mexico: Yucatan, Quintana Roo and Campeche, western Cuba.

MEXICO. Yucatan, Mpio. of Yaxcabá, 5 March 1979, *Arias & Vara* 113 (MEXU!); c 31.5 km along road Peto to Tixcacaltuyab, 24 Feb. 1979, *Arias & Vara* 78 (MEXU!); 3 km S of Libre Unión, road to Yaxcabá, 17 April 1986, *Cabrera & Cabrera* 11277 (MEXU!); 6 km W of Timun, road to Dzitas, 17 April 1986, *Cabrera & Cabrera* 11243 (MEXU!, TEX!); 24 km SW of Tzucacab, road to Becanchen, 20 April 1986, *Cabrera & Cabrera* 11334 (MEXU!); WNW of Poxila, 4 Jan. 1956, *Enriquez* 288 (MEXU!, US!); Cenotillo, 7 April 1956, *Enriquez* 547 (MEXU!); Kancabzonot, March 1917, *Gaumer* s.n. 23628 (F!, US!); San Anselmo, without date, *Gaumer* 1623 (F!, GH!, NY!, US!); Izamal, 1895, *Gaumer* 349 (BR!, E!, F!, K!, NY!); 1917--1921, *Gaumer* 24140 (F!); Izamal, 1888, *Gaumer* s.n. (K!); Izamal, 22 Feb. 1906, *Greenman* 462 (F!); c 25 km N of Valladolid, near village of Santa Rita, 28 March 1987, *Hughes* 941 (FHO, K!); c 30 km S of Valladolid near village of Tixcacalcupul, 4 March 1989, *Lewis & Hughes* 1764 (BR!, FHO!, K!, MEXU!, NY!, US!); road Campeche to Mérida, near Chencoyi, 16 March 1968, *Pennington & Sarukhan* 9568 (K!, NY!); Mpio. Yaxcabá, 29 April 1981, *Vargas & Sima* 405 (F!); S of Ticul, 22 Feb. 1982, *White & Mott* 105 (MEXU!); near Calcehtok, 21 Feb. 1982, *White & Mott* 82 (MEXU!); Yokdzonot Presentados, 60 km from Mpió. de Tizimin, 16 April 1986, *Zepeda et al.* 194 (MEXU!); **Quintana Roo,** Cobá, 2 km E of Nohoch Mull, 17 Feb. 1975, *Barrera et al.* s.n. (MEXU!); rancho Dos Fierros, near Puerto Morelos,10 March 1984, *Cabrera & Cabrera* 6306 (MEXU!, NY!); 5 km S of the urban zone of Isla de Mujeres, 18 Sept. 1985, *Cabrera & Cabrera* 9247 (MEXU!); Tres Reyes, 12 Nov. 1980, *Cabrera & Cortez* 274 (MEXU!); Isla de Cozumel, 13 March 1986,*Cabrera & Téllez* 11071 (MEXU!); 14 March 1986, *Cabrera & Téllez* 11126 (MEXU!); 8 km S of Akumal, 13 March 1981, *Cabrera & Zarate* 1467 (MEXU!); Mpio. Xcaret, road to Hotel Marina Azul off Cancún to Chetumal road, 2 March 1985, *Cowan & Cabrera* 5087 (MEXU!); Mpio. Carillo Puerto, km 12 from Vigía to Carillo Puerto, 29 Feb. 1984, *Durán & Olmsted* 849 (MEXU!); km 17 from Vigía to Carillo Puerto, *Durán & Olmsted* 846 (MEXU!); Xel-Ha, 20 Aug. 1976, *Grether* 441 (MEXU!); 20 km ENE of Filipe Carillo Puerto, road to Vigía Chico, 31 Aug. 1979, *Grether et al.* 1314 (MEXU!); 3 km E of Vicente Guerrero on road from Cancún to Valladolid, 1 Feb. 1985, *Hughes* 492 (K!, MEXU!); c 35 km N of Chetumal on highway 307 to Felipe Carillo Puerto, 4 March 1989, *Lewis & Hughes* 1762 (BR!, FHO!, K!, MEXU!, NY!); S of rancho San Martín, 22 March 1976, *Moreno* 561 (K!, MEXU!); 6 km SW of Puerto Morelos, 1 Feb. 1980, *Sousa et al.* 11003 (MEXU!); 3 km W of San Luis on road Polyuc to Felipe Carillo Puerto, 18 May 1982, *Sousa et al.* 12435 (MEXU!); 4 km W of Vallarta, 5 May 1982, *Sousa et al.* 12329 (MEXU!); 7 km S of Puerto Morelos, 4 April 1980, *Téllez & Cabrera* 1883 (MEXU!); 2 km S of Puerto Morelos, 4 April 1980,*Téllez & Cabrera* 1871 (MEXU!); road to Laguna Ocom, 10 Jan. 1980, *Téllez & Cabrera* 1200 (MEXU!); 10 km N of Bacalar, 14 Oct. 1980, *Téllez & Cabrera* 3649 (MEXU!); Puerto Morelos, Jardin Botánico, 15 March 1984, *Uitzil et al.* 15 (MEXU!); **Campeche,** 4 km S of Dzibalanchen, 30 March 1982, *Cabrera & Cabrera* 2361 (MEXU!); road Campeche to Mérida, W of Hopelchen, 14 March 1954, *Miranda* 7969 (MEXU!, US!); 30 km N of Campeche, 16 May 1968, *Pennington & Sarukhán* 9624 (K!); Tikinmul on Mérida to Campeche road, 28 Feb. 1958, *Schubert &*

Gomez Pompa 1683 (MEXU!); **BELIZE**, Corozal Dist., between Sarteneja and Chunox, 18 March 1987, *Davidse & Brant* 32646 (K!); vicinity of Little Belize, 17 March 1987, *Davidse & Brant* 32600 (MEXU!); road to Altun Ha from Northern Highway, c mile 32, 2 June 1974, *Dwyer* 12573 (MEXU!, NY!); Belize to Cayo road, 1 April 1958, *Gentle* 9707 (LL!, MEXU!); Salt Creek, without date, *Hammel* 122 (K!); Freshwater Creek, 1928, *Heyder & Kinloch* 29 (F!); Freshwater Creek, 9 June 1928, *Kinloch* 6 (F!); El Cayo, 11 km from Belmopan to Belize City, 1 March 1991, *MacQueen & Pennington* 90 (EAP, FHO, K!, MEXU, MO); 1927, *Winzerling* X--4 (F!); 10 Oct. 1926, *Winzerling* V--3 (F!); **CUBA**, Remates de Guane, Pinar del Rio, El Cayuco, April 1926, *Fors* 3965 (HAC!, NY!).

ECOLOGY. Low to medium stature semi-deciduous, seasonally dry forest; sea level to 150 m.

PHENOLOGY. Flowering principally from January to April, less frequently later in the year (records for June and October), fruiting January to May with fruits sometimes persisting until November.

VERNACULAR NAMES. "Peccary wood", "warrie wood" (Belize); "Palo jabali", "Kitam-ché" (Quintana Roo); various orthographic variants of "Kitam-ché" and "Citinché" (Yucatan and Campeche) e.g. "Citamche", "Xkitamche" and "Xcitinché"; citin=furnace, ché=tree, the name perhaps alluding to the use of the wood as charcoal. The wood is reported to smell like peccaries (*Hammel* 122), thus the vernacular name in Belize.

NOTES. The flowers are recorded as having a slightly peppery scent (*Lewis & Hughes* 1762). Gaumer reported that the larger trees make very fine telegraph poles (*Gaumer* 23628).

In the Mexican state of Oaxaca, between Tehuantepec and Niltepec, several collections represent a distinct form of *Caesalpinia gaumeri* with larger flowers and a reduced number of pinnae per leaf. Given the disjunct geographical distribution and slight morphological differences a new subspecies of *C. gaumeri* is indicated, but more collections need to be made before a final decision can be made.

Two fruiting collections from Peru, *Smith* 6159 and *Vega* 5182, perhaps represent a new species, related to *C. gaumeri*, but flowering material is needed to confirm this. Both collections come from the Celedin Province in the Department of Cajamarca.

22. **Caesalpinia pinnata** (*Griseb.) C. Wright* in Sauv. Anal. Acad. Habana 5: 404 (1869). Type: Cuba, *Wright* 2360 (holotype GOET!, isotypes GH!, K!, NY!).
Libidibia pinnata Griseb., Cat. Pl. Cub.: 79 (1866). (As '*Lebidibia pinnata*').
Caesalpinia oblongifolia Urban, Symb. Ant. 2: 281 (1900). Type as for *C. pinnata*.
Poincianella pinnata (Griseb.) Britton & Rose in N. Amer. Fl. 23(5): 335 (1930).
Poincianella oblongifolia (Urban) Britton & Rose, loc. cit. (1930).
Poincianella savannarum Britton & Wilson, loc. cit. (1930). Type: Cuba, Sancti Spiritus, 20 July 1915, *León & Roca* 7835 (holotype NY!).
Caesalpinia savannarum (Britton & Wilson) León in Contrib. Ocas. Mus. Hist. Nat. Col. 'de la Salle', Habana 10 (Fl. Cub. 2): 283 (1951).
Caesalpinia oblongifolia var. *savannarum* (Britton & Wilson) A. Borhidi & O. Muniz in Bot. Kozlem. 62(1): 25 (1975).

Unarmed shrub, c 30 cm - 4.5 m tall; young stems and foliage sometimes pubescent with the pubescence persisting on the leaflet main vein and occasionally sparsely so on the blade surfaces. *Leaves* pinnate; petiole 0.6--2.2 cm long; rhachis 1.8--5.6(--12) cm long; leaflets (3--)4--18 per leaf, usually in opposite pairs, coriaceous, oblong-elliptic, oblong-ovate to suborbicular, apex rounded to emarginate, base oblique, inequilaterally cordate to subtruncate, terminal leaflets 1.6--3.5 x 1--2.6 cm, median leaflets 1.5--4.7 x 1.1--2.5 cm, usually glabrous; venation prominent on both surfaces, secondary veins brochidodromous, tertiaries reticulate; scattered, dark, subepidermal glands on leaflet surface, these obscure on mature leaves, sometimes very evident along the margin which is then crenulate. *Inflorescence* an 8--24-flowered terminal (less often axillary) raceme, glabrous or finely pubescent with white ± incurved hairs; bracts early caducous; pedicels 1--2.2 cm long, articulated 2--3 mm below calyx base. *Calyx* lobes 4.5--7 mm long, finely pubescent, black subepidermal glands scattered over surface, lower lobe slightly cucullate. *Corolla* bright yellow; standard blade broadly orbicular, wider than long, 10--12 x 8--13 mm (including a 2--3 mm claw), base of blade with inrolled flaps, claw and blade base glandular, claw pubescent; upper lateral petals 11--16 x 9--11 mm (including a 1.5--2 mm claw); lower laterals 12--16 x 9--10 mm (including a 1.5--2 mm claw), claw and blade base of all laterals glandular. Stamen filaments 9--13 mm long, pubescent and glandular on basal $^1/_2$--$^2/_3$; anthers 1--1.5 x 0.75 mm. Ovary moderately to densely pubescent,

sparsely glandular, 4--5-ovulate; style c 9 mm long, slightly expanded near apex; stigma a terminal, fringed chamber. *Fruit* an elastically dehiscent, subligneous pod, 3.2--5.5 x 0.9--1.4(--2.2) cm (including a beak of c 6 mm), the valves twist after dehiscence, finely pubescent (especially the suture of young fruits) to glabrous, eglandular or glandular with sessile glands, nitid, 3--5-seeded. *Seeds* ovate-orbicular, 8 x 6.5 x 2 mm, olive-brown, shiny. (Fig. 5R, 39, Map 14).

DISTRIBUTION. Endemic to Cuba.

CUBA: Prov. Las Villas, SE of Sancti Spiritus, 29 Aug. 1950, *Alain* 1598 (HAC!); Prov. Guantánamo, 3 km W of Imías, 10 May 1980, *Alvarez et al.* 43042 (HAJB!); Prov. Cienfuegos, Aguada de Pasajeros N of the national highway, km 193, 28 March 1980, *Bisse et al.* 41731 (HAJB!); Prov. Guantánamo, Maisi, Boca de Jauco, 2 June 1982, *Bisse et al.* 47482 (HAJB!); Prov. Santa Clara, Rio Arimao, 22 March 1910, *Britton & Wilson* 5765 (NY!); Casilda, 16 March 1910, *Britton & Wilson* 5593 (NY!); Prov. Oriente, Imías, July 1936, *Bucher* 10104 (HAC!); Prov. Oriente, Papayo, 20 July 1918, *Ekman* 9430 (US!); Santa Clara, near Motembo, 28 June 1923, *Ekman* 16845 (NY!); Santa Clara, near Manacas, June 1941, *Howard* 5547 (NY!); Gerhartz farm, 12 km E of Cascajal, June 1941, *Howard* 5577 (GH!, NY!); Hormiguero, 15 March 1933, *Jack* 8719 (A!); same locality, 28 March 1932, *Jack* 8630 (A!, NY!); Soledad, Cienfuegos, 23 March 1932, *Jack* 8639 (NY!); Santa Clara, SE of Sancti Spiritus, Playa de Romero, 28 June 1932, *León* 15649 (HAC!, NY!); S of Sancti Spiritus, near Guasimal, 26 June 1931, *León* 14919 (HAC!, NY!); Prov. Oriente, S Baracoa region, ? Junco, 17 July -- 4 Aug. 1924, *León* 11653 (GH!, HAC!, NY!); Santa Clara, Gaza del Sur, 14 Aug. 1916, *León* 6731 (NY!); Gaza, 25 Aug. 1909, *León* 1307 (NY!); Sancti Spiritus, 20 July 1918, *León & Roca* 7835 (NY!); Prov. Oriente, laguna Macambo, 16 June 1972, *Risso et al.* 27547 (HAC!); Prov. Las Villas, sabanas de Cascajal, 8 June 1948, *Roig* 23613 (HAC!); Baracoa, 5 July 1860--64, *Wright* 2360 (holotype GOET!, isotypes GH!, K!, NY!); Baracoa, Oct. 1965, *Yero* 628 (HAC!); Prov. Las Villas, S of Sancti Spiritus, June 1966, *Yero* 771 (HAC!); same locality, May 1966, *Yero* 26047 (HAC!).

ECOLOGY. Coastal thickets on sandy plains and rocky hillsides.

PHENOLOGY. Flowering and fruiting from March to August.

VERNACULAR NAME. "Clavellina de costa".

NOTES. Leaflet shape and number per pinna (or per leaf in this instance) vary greatly in species of *Caesalpinia* and there seems no good reason for retaining *C. pinnata, C. oblongifolia* and *C. savannarum* as separate species based on minor foliage characters. Borhidi and Muniz (1975) had already down-ranked *C. savannarum* to a variety of *C. oblongifolia* and Barreto Valdés (pers. comm. 1990) confirms that the three species names

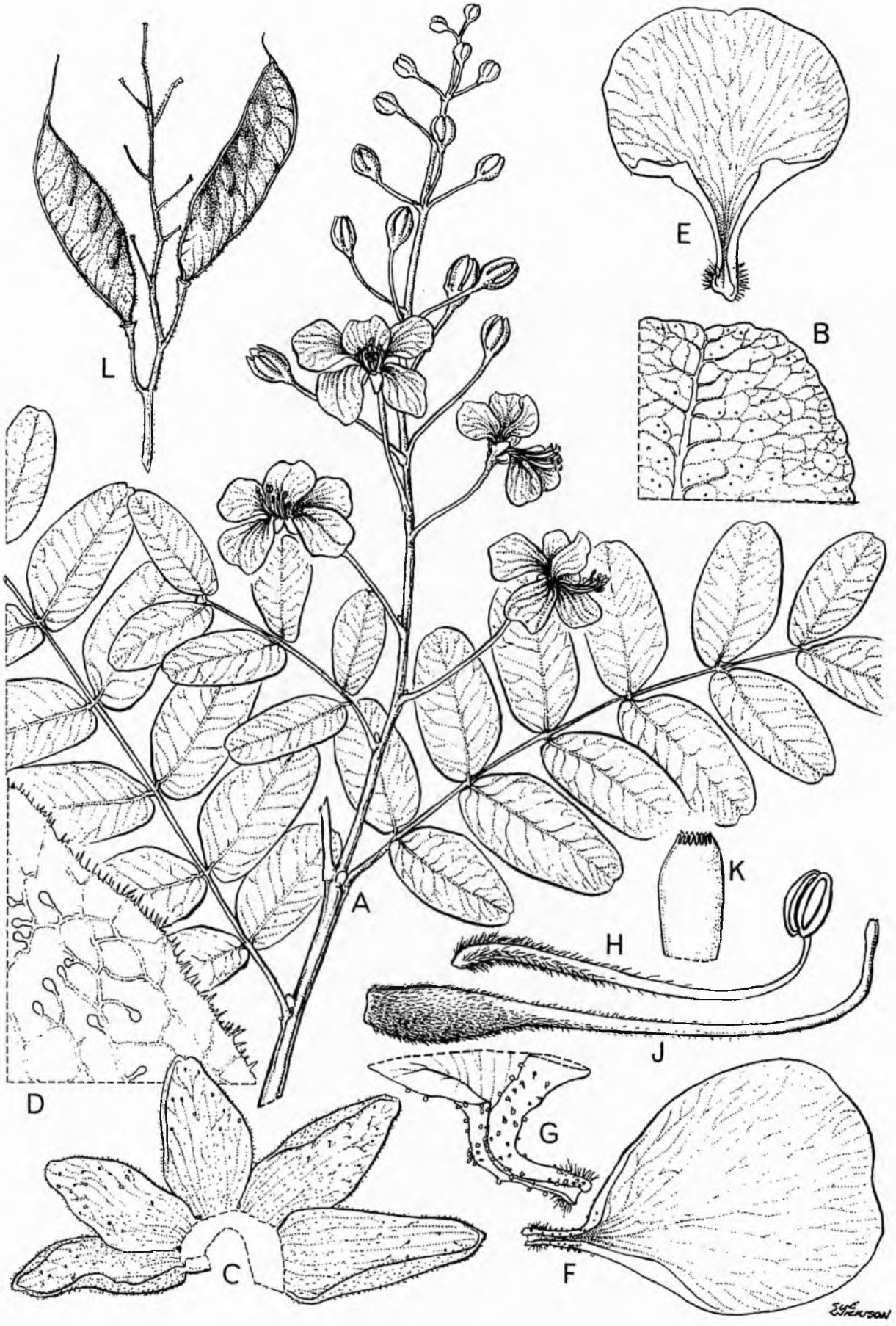


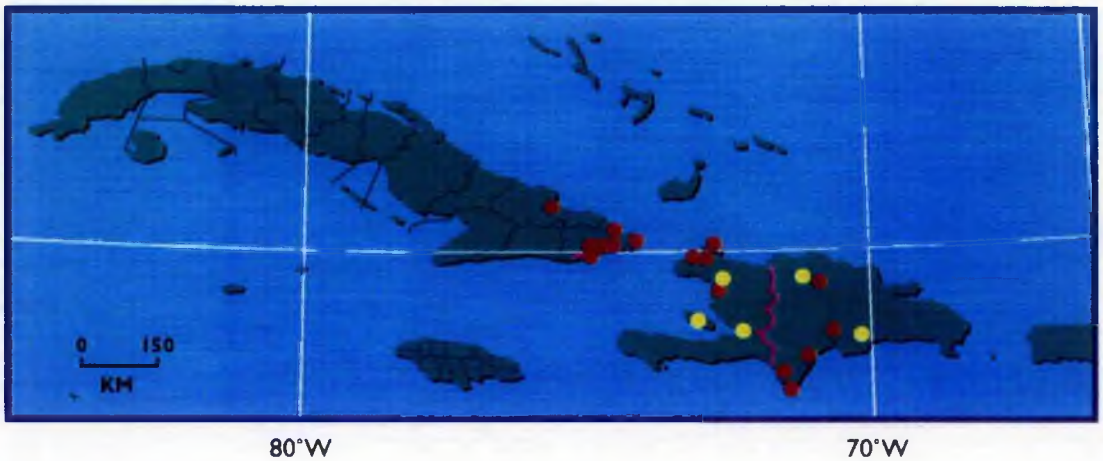
FIG. 39. *Caesalpinia pinnata*. **A** inflorescence and foliage x 1; **B** leaflet undersurface detail x 4½; **C** calyx opened out x 6; **D** calyx lobe margin detail x 30; **E** standard petal x 6; **F** lateral petal x 6; **G** lateral petal claw x 12; **H** stamen x 9; **J** gynoecium x 9; **K** stigma x 40; **L** fruits x 1. **A** & **B** from *Howard* 5577, **C–K** from *Jack* 8719, **L** from *Jack* 8630. Drawn by Sue Wickison.

Map 14

Distribution of *Caesalpinia pinnata* (●) *C. myabensis* (○) and *C. nipensis* (●) in Cuba

Map 15

Distribution of *Caesalpinia glandulosa* (●) and *C. pellucida* (○) in Cuba and Hispaniola



represent only forms of one species. *C. pinnata* and *C. oblongifolia* are, in fact, based on the same type, *Wright* 2360. *C. pinnata*, as currently recognised, is closely related to *C. myabensis*, also from Cuba, which essentially differs in having bipinnate leaves with correspondingly smaller leaflets.

23. **Caesalpinia myabensis** *Britton* in Mem. Torrey Bot. Club 16: 66 (1920). Type: Cuba, Oriente, between Holguin and Myabe, April 1909, *Shafer* 1403 (holotype NY!, isotype A!).

Libidibia pauciflora Griseb. var.? *puberula* Griseb. Cat. Pl. Cub.: 79 (1866). Type: Cuba, *Wright* 2362 (incorrectly given as '1362').

Caesalpinia subglauca Britton in Mem. Torrey Bot. Club 16: 66 (1920). Type: Cuba, Oriente, near Santiago, *Britton et al.* 12596 (holotype NY!).

Caesalpinia hornei Britton, loc. cit.: 67 (1920). Type: Cuba, Ciego de Avila, Camaguey, 3 Sept. 1905, *Horne* 95 (holotype NY!).

Poincianella myabensis (Britton) Britton & Rose in N. Amer. Fl. 23(5): 334 (1930).

Poincianella subglauca (Britton) Britton & Rose, loc. cit.: 333 (1930).

Poincianella hornei (Britton) Britton & Rose, loc. cit.: 333 (1930).

Poincianella clementis Britton, loc. cit.: 333 (1930). Type: Cuba, Oriente, Renté, Santiago, July 1919, *Clement* 135 (holotype NY!, isotype HAC!).

Caesalpinia clementis (Britton) León in Contrib. Ocas. Mus. Hist. Nat. Col. 'de la Salle', Habana 9: 12 (1950).

Caesalpinia hermeliae León, loc. cit.: 12 (1950). Type: Cuba, Oriente, SW of Holguin, orillas del monte de Caguairanal, 18 March 1932, *León & Garcia* 15501 (holotype LS, isotypes HAC!, NY!).

Caesalpinia myabensis var. *clementis* (Britton) Barreto in Acta Botanica Cubana 89: 6 (1992).

Caesalpinia myabensis var. *hermeliae* (León) Barreto, loc. cit.: 5 (1992).

Caesalpinia myabensis var. *hornei* (Britton) Barreto, loc. cit.: 5 (1992).

Caesalpinia myabensis var. *subglauca* (Britton) Barreto, loc. cit.: 6 (1992).

Unarmed multiple-stemmed shrub, 1--4 m tall, stems up to 5 cm in diam.; bark whitish-grey; scattered ovate-orbicular lenticels on young branchlets, young shoots finely pubescent, sometimes black glands amongst indumentum of young leaf rhachides. *Leaves* bipinnate; petiole (3--)12--25 mm long; rhachis 1.8--5 cm long; pinnae in 1--4 opposite to alternate pairs, plus a terminal pinna, leaflets 7--17 per pinna, alternate to opposite (on terminal pinna), sclerophyllous, oblong-elliptic, narrowly elliptic, suborbicular to subrhomboid, apex shallowly emarginate, base subtruncate, the main vein subcentric, terminal leaflets 6--24 x (2.5--)5--16 mm, medians 6--21 x 4--13 mm, upper surface of blade nitid, glabrous to sparsely spreading pubescent or with only the primary and secondary veins pubescent, lower surface glabrous or with a few scattered hairs on main vein and margin; venation prominent on both surfaces, secondary veins brochidodromous, tertiaries reticulate, a marginal vein usually evident; sparse, black, subepidermal glands scattered between the tertiary veins on the lower surface (these more evident on juvenile leaflets). *Inflorescence* an axillary or teminal, c 14--30-flowered, lax raceme, the rhachis pubescent with short, curled white hairs, glabrescent; pedicels c 12--22(--24) mm long, articulated just below to 5 mm below calyx. *Calyx* lobes 5--8 mm long, finely pubescent, black subepidermal glands scattered over surface. *Corolla* yellow, standard petal blade ± orbicular, c 10--15 x 8--13 mm (including a 3--4 mm claw) apex emarginate and ± dentate, a few subepidermal glands in blade especially near apex, base of blade folded upwards, claw without apical ridge or appendage but inner face and margins at base densely pubescent, margins stipitate-glandular; upper lateral petals broadly obovate, c 13 x 9.5 mm (including a 3 mm claw), apex rounded to shallowly emarginate, lower laterals c 12 x 8 mm (including a 2.5 mm claw), all laterals with a few subepidermal glands in blade, claws densely pubescent on inner surface, margins and blade margin at base stipitate-glandular. Stamen filaments 8--14 mm long, pubescent on basal $^1/_2$--$^3/_4$, short stipitate-glandular; anthers 1.5 x 0.5--0.75 mm. Ovary densely pubescent with a few glands intermixed especially in upper $^1/_2$; style 8--9 mm long; stigma a terminal, funnel-shaped, fringed chamber. *Pod* subligneous, elastically dehiscent,3.8--5 x 1.2--1.5 cm (including a narrow beak up to 5 mm long); valves twist after dehiscence, short, spreading, white pubescent, glabrescent (hairs most evident on the suture), sparse to dense reddish, sessile glands scattered over surface or only evident near the base, c 2--4-seeded. (Figs. **40** & 43F, Map 14).

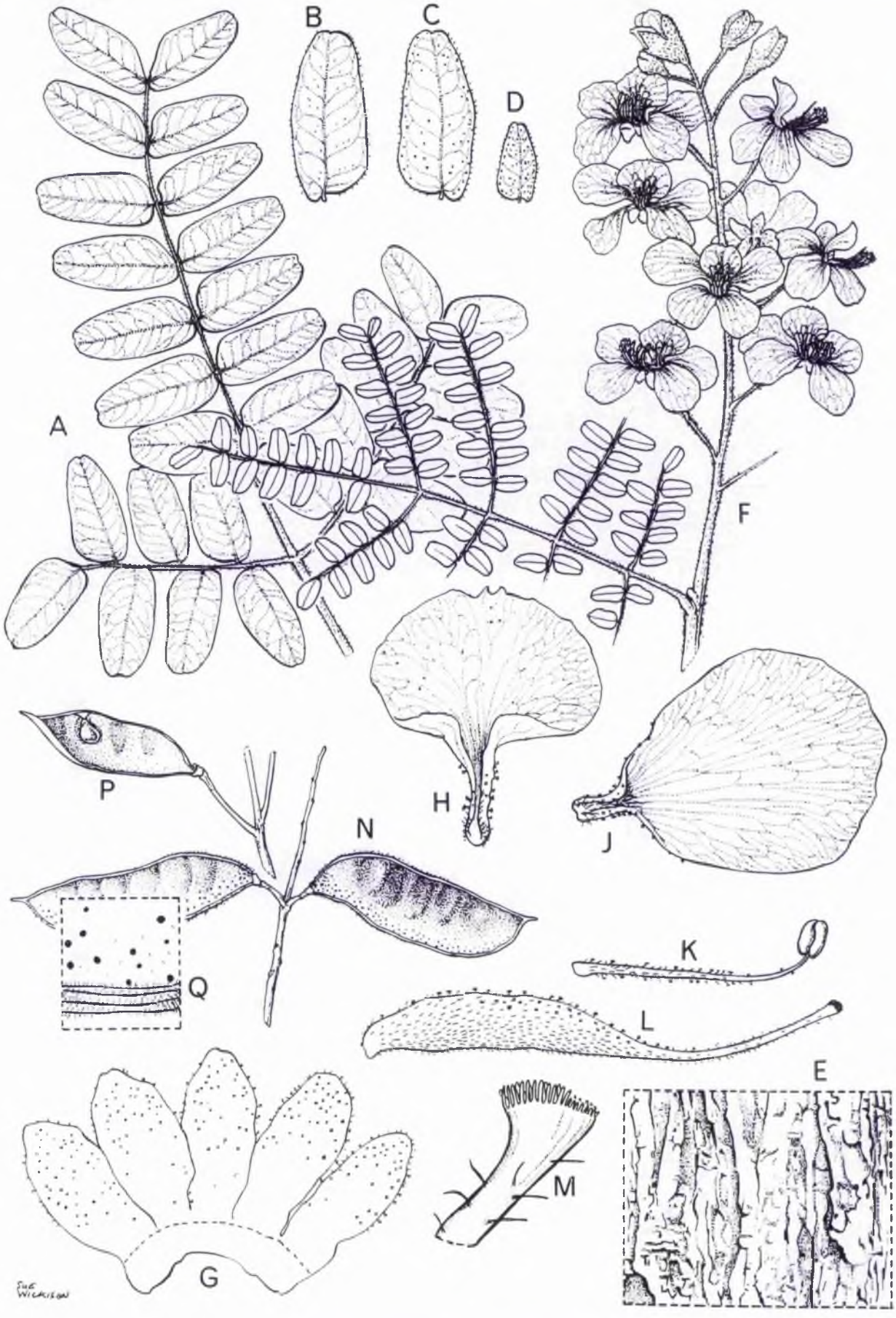


FIG. 40. *Caesalpinia myabensis*. **A** bipinnate leaf x 1; **B–D** leaflet undersurfaces to show range and sunken idioblasts x 1½; **E** bark section x 1½; **F** inflorescence and foliage x 1; **G** calyx opened out x 4½; **H** standard petal x 4½; **J** lateral petal x 4½; **K** stamen x 4½; **L** gynoecium x 4½; **M** stigma x 15; **N** fruits x 1; **P** twisted fruit valve x 1½; **Q** detail of fruit margin showing glands x 6. **A–C** from *Ekman* 15585, **D** & **N–Q** from *Shafer* 1403, **E** from *Lewis* 1845, **F–M** from *Bailey* 15120. Drawn by Sue Wickison.

DISTRIBUTION. Endemic to Cuba.

CUBA: La Ciega, Caobilla, Camaguey, 23--25 June 1927, *Acuña* 16990 (HAC!); Prov. Camaguey, La Entrada, Florida, 1 Jan. 1950, *Acuña* 15883 (HAC!); Vertientes, 11 Nov. 1950, *Acuña* 16479 (HAC!); Playa de Gibara, Oriente Mayo, 20 May 1955, *Acuña & Zayas* 19664 (HAC!, HAJB!); Prov. Oriente, nr. V. de las Tunas, 15 June 1953, *Acuña & Correll* 18680 (HAC!); Prov. Habana, Jaruco, 20 Nov. 1979, *Alvarez* 41681 (HAJB!); Prov. Holguin, Banes, N of Cañadon, 19 Oct. 1978, *Alvarez et al.* 38352 (HAJB!); near Holguin, 8 March 1931, *Bailey* 15120 (NY!); Prov. Camaguey, Guaimaro, N of Monte Grande, 12 May 1976, *Bisse et al.* 31442 (HAJB!); Oriente, nr. Santiago, 10--25 March 1912, *Britton et al.* 12596 (NY!); Santiago de Cuba, Loma Colorado, 7 May 1932, *Bucher* 307 (NY!); Holguin, Aug. 1929, *Bucher* 17000 (HAC!); Santiago de Cuba, Renté, May 1943, *Chrysogone* 2687 (HAC!); Renté, April 1947, *Clemente* 5306 (HAC!); May 1943, *Clemente* 2682 (HAC!); Siboney to Sardinero, April 1949,*Clemente* 6523 (GH!, US!); Renté, July 1919, *Clemente* 135 (HAC!, NY!); Bahia de Santiago de Cuba, April 1847, *Crisogono* 5360 (HAC!); Victoria de las Tunas, 27 Oct. 1922, *Ekman* 15585 (A!, K!, NY!); Gamboa, 28 Aug. 1922, *Ekman* 14991 (NY!); nr. Cacocúm, 10 March 1956, *Figueiras* 2604 (HAC!, HAJB!); Ciego de Avila, 3 Sept. 1905, *Horne* 95 (NY!); road to Aguadores, Santiago de Cuba, 6 Aug. 1935, *León* 16398 (GH!); Camaguey, Sabana de Velasco, 4 Aug. 1934, *León* 16133 (HAC!); NE of Victoria de las Tunas, 5 July 1932, *León* 15766 (GH!, HAC!, NY!); Guirabita, road to Holguin, 18 March 1932, *León & Garcia* 15501 (HAC!, NY!); Aguadores, 17 April 1940, *León et al.* 17689 (HAC!); Holguin Prov., Mpio. Banes, 2--3 km from Cañadon to Guardalavaca, 9 July 1990, *Lewis et al.* 1845 (G!, HAJB!, K!, NY!); between Holguin and Myabe, April 1909, *Shafer* 1403 (holotype NY!, isotype A!); without exact locality, 1860--64, *Wright* 2362 (GH!, K!).

ECOLOGY. Coastal and dry hillside thickets, sandy savannas, ?0--120 m.

PHENOLOGY. Poorly-known but apparently flowering from January to November, fruiting collections made in October, March, May, June and July.

NOTES. In the 1920s many new species of *Caesalpinia* were described from Cuba by Britton and in the 1930s these were given new combinations in *Poincianella* by Britton and Rose. Those related to *C. myabensis* were distinguished by leaflet number, size, shape and indumentum but in a genus where such characters vary greatly within a population of a single species they cannot be used to justify the recognition of separate species. Barreto (1992) in Cuba has chosen to recognise all of the species placed in synonymy under *C. myabensis* in this work as varieties of it. I have chosen not to recognise the variable vegetative forms as infraspecific taxa. Furthermore, *C. pinnata*, as recognised in this account, differs from *C. myabensis* essentially only in having once pinnate leaves with usually opposite leaflets. In *C. myabensis* leaflets are alternate to opposite, but always

opposite on the single terminal pinna; the leaflets are usually smaller but when the bipinnate leaf is reduced to one pair of pinnae plus a terminal pinna the size of the leaflets is correspondingly greater - an apparent progression towards the larger leafleted *C. pinnata*. Pending further field study *C. pinnata* and *C. myabensis* are kept separate but it seems reasonable to suggest that they are probably just forms of the same species.

24. **Caesalpinia pellucida** *Vogel* in Linnaea 10: 601 (1836). Type: Dominican Republic, *Ehrenberg* s.n. (isotype NY!).
Poincianella pellucida (Vogel) Britton & Rose in N. Amer. Flora 23(5): 334 (1930).

Unarmed shrub to 2.5 m tall; young stems and leaf rhachides finely pubescent, stellate indumentum on very young foliage. *Leaves* bipinnate; stipules filiform, c 1.5 mm long, pubescent, early caducous; petiole 0.8--2.5 cm long; rhachis 6.5--12.5 cm long, pubescent, glandular, occasionally with a few stellate hairs intermixed; pinnae in 5--9 opposite to alternate pairs plus a terminal pinna; leaflets alternate, 12--17 per pinna, suborbicular, subrhomboid to oblong-elliptic, apex short-apiculate, less often rounded or obtuse, base inequilaterally truncate, 7.5--11 x 5--8 mm, sparsely puberulous on both surfaces, the lower surface sometimes with a few obscure stellate hairs, or sometimes ± glabrous; secondary venation brochidodromous, prominent on upper surface, tertiary venation reticulate; main vein terminating in a glandular tip, lower surface of blade with scattered dark reddish-black subepidermal glands. *Inflorescence* a 15--18-flowered axillary or terminal raceme, the rhachis finely pubescent; bracts early caducous (not seen); pedicel c 14--16 mm long. *Calyx* lobes 5.5--6.5 mm long, outer surfaces finely pubescent, inner surfaces densely silky tomentose, margins with stalked glands, the stalks pubescent, scattered subepidermal dark glands in lobes. *Corolla* yellow; standard blade transverse-elliptic, wider than long, 12--13 x 10--12 mm (including a 3.5--4 mm claw), blade eglandular, claw thickened, ± inrolled, pubescent, stipitate-glandular; upper lateral petals broadly obovate, apex truncate, 13--14 x 9--10 mm (including a 2 mm claw); lower lateral petals obovate, apex truncate, 14--15 x 9--10 mm (including a 2 mm claw), all laterals with claws pubescent on inner surface, stipitate-glandular on margins and outer surface,

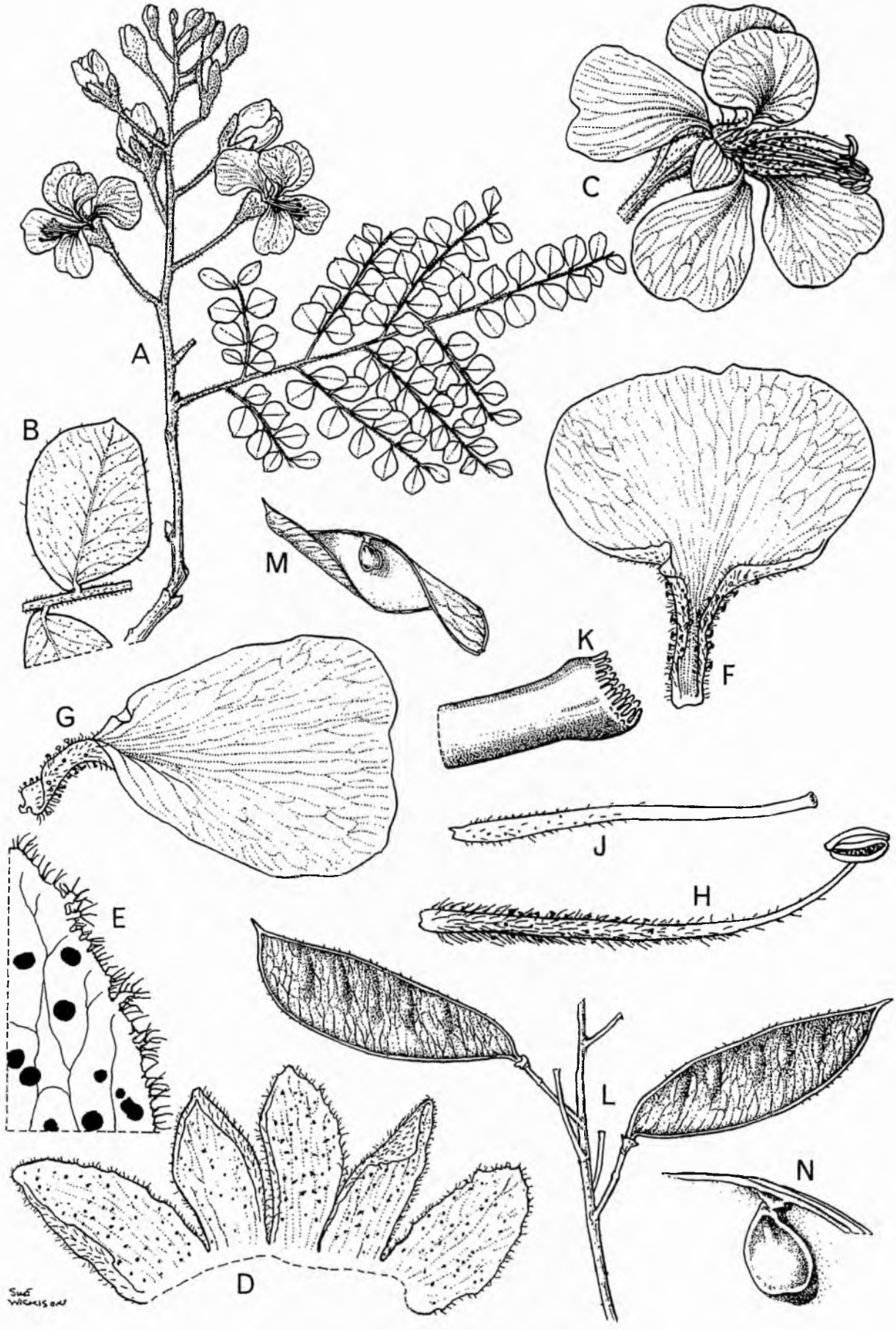


FIG. 41. *Caesalpinia pellucida*. **A** inflorescence and bipinnate leaf x 1; **B** leaflet undersurface x 4½; **C** flower x 3; **D** calyx opened out x 6; **E** detail of calyx lobe margin x 40; **F** standard petal x 6; **G** lower lateral petal x 6; **H** stamen x 9; **J** gynoecium x 9; **K** stigma x 40; **L** fruits x 1; **M** twisted fruit valve x 1; **N** seed x 3. **A** & **C–K** from *Ekman* H4999, **B** & **L–N** from *Liogier* 18510. Drawn by Sue Wickison.

blades eglandular. Stamen filaments 10--11 mm long, pubescent on basal $^1/_2$--$^2/_3$, glandular; anthers 1.5 x 0.75 mm. Ovary densely short-pubescent with pale, sessile glands intermixed; stigma a slightly flared, fringed, terminal chamber. F*ruit* an elastically dehiscent pod, 5.8--7 x 1.3--1.7 cm (including a 4--7 mm acuminate beak), finely pubescent, glabrescent, eglandular or with very sparse dark red, sessile globular or doughnut-shaped glands scattered over surface, valves twist after dehiscence, c 4-seeded. (Fig. **41**, Map 15).

DISTRIBUTION. Haiti and the Dominican Republic.

HAITI: Gros Morne, road to Chapelle Moulin, 3 Oct. 1925, *Ekman* 4999 (GH!, K!, US!); Gonave Island, near Etroite, 15--21 March 1920, *Leonard* 3415 (US!); near Port au Prince, 19--23 May 1929, *Leonard & Leonard* 15874 (NY!); without exact locality or date, *Picarda* 18 (K!); **DOMINICAN REPUBLIC**, Prov. Santiago, Mao, 23 Feb--1 March 1921, *Abbott* 1057 (GH!, NY!); without exact locality or date, *Ehrenberg* s.n. (NY!); *Jäger* s.n. (BR!); on Najayo road, Nigua, 24 March 1972, *Liogier* 18510 (NY!).

ECOLOGY. In thickets on limestone, 50--350 m.

PHENOLOGY. Flowering February and March (one record for October), fruiting February to May.

NOTES. A seldom collected and thus little-known species having affinities with *C. pinnata* and *C. myabensis* from Cuba.

25. **Caesalpinia nipensis** *Urban*, Symb. Ant. 9: 444 (1928). Type: Cuba, Prov. Oriente, Sierra de Nipe, 27 April 1919, *Ekman* 9572 (holotype S!, isotype NY!).
Poincianella nipensis (Urban) Britton in N. Amer. Fl. 23(5): 335 (1930).

Unarmed shrub to small tree, 1--10 m tall, single or multiple-stemmed, main trunks c 5 cm in diameter, main stems and branches sometimes zig-zag; bark brown, black or grey or mottled a mixture of these colours; wood hard and dense; young branchlets with dense, vertically arranged pustular lenticels, glabrous. *Leaves* bipinnate; stipules foliaceous, c 2 mm long, pubescent, the margin somewhat dentate, early caducous; petiole (3--)8--10 mm long; rhachis 2--8 cm long; pinnae in 2--3 opposite pairs (single terminal pinna lacking);

petiolules 1.5--3 mm long, leaflets in 3--5 opposite pairs, broadly elliptic to obovate, apex rounded to obtuse, base slightly asymmetric, 2.5--6 x 1.5--3.8 cm, nitid, glabrous but for an occasional small tuft of hairs at the base of the subcentral main vein, distinctly discolourous when dry, secondary venation brochidodromous, tertiary venation finely reticulate, thickened marginal vein causing margin of leaflet to be ± revolute; scattered, black, subepidermal glands dense on lower surface of leaflet, these sometimes obscure. *Inflorescence* an axillary or short, pseudolateral raceme, glabrous, c 6--20-flowered; pedicels 8--14 mm long, articulated 1.5--2.5 mm below calyx. *Calyx* lower lobe ± cucullate, up to 8.5 mm long, the other four 4.5--5 mm long, the hypanthium glabrous, the lobes finely pubescent on both surfaces, with scattered pale, globular, subepidermal glands. *Corolla* yellow; sparse, whitish, globular, subepidermal glands in blades of all five petals; standard with orangish-red network of veins, blade broadly triangular, obovate or suborbicular, 10--16 x 6.5--7 mm (including a 3.5--5 mm pubescent claw); upper lateral petals with broadly obovate blade, 11--16.5 x 7--8 mm (including a 2--3 mm claw); lower laterals broadly obovate, 11--16.5 x 8 mm (including a 1.5--3 mm claw). Stamen filaments with an indumentum of thick, transparent hairs for $^{2}/_{3}$--$^{3}/_{4}$ of their length, eglandular; anthers crimson to deep purplish-red, 1--1.5 x 0.5--0.75 mm. Ovary glabrous, 2-ovulate; style c 11 mm long; stigma a terminal fringed chamber. *Fruit* a dehiscent, subligneous pod, up to 3.5 x 1.7 cm, valves glabrous, rolling up after dehiscence, 1--2-seeded. *Seeds* subcordate to ovate, 7--10 x 6--7 x 1.5--2 mm, olive-brown. (Figs. **42** & 43A-E, Map 14).

DISTRIBUTION. Endemic to eastern Cuba.

CUBA. Prov. Oriente, Pinares, vicinity of Moa, 10 April 1945, *Acuña* 12432 (HAC!, US!); Moa, Playa Vaca, 4 Nov. 1945, *Acuña* 13111 (HAC!); Orillas del Rio Miguel, 2--7 April 1956, *Alain et al.* 5891 (HAC!); Prov. Holguin, Moa, La Breña, 7 May 1973, *Alvarez & Berazain* 24428 (HAJB!); Prov. Holguin, Moa, km 6 on road from La Melba to Rio Quesigua, 1 May 1980, *Alvarez et al.* 42502 (HAJB!); Prov. Oriente, Moa, June 1967, *Bisse & Rojas* 4295 (HAJB!); road Breña to Moa, 14 April 1981, *Bisse et al.* 44112 (HAJB!); Moa, Punta Gorda, 18 Feb. 1970, *Borhidi et al.* 96/37 (HAC!); Sierra de Iberia, Santa Maria, Bahia de Taco, 22 March 1970, *Borhidi et al.* 120/12 (HAC!); Moa, 26 June 1945, *Clemente* 4372 (HAC!); Rio Cayoguán, July 1979, *Clemente et al.* 6796 (HAC!); Sierra de Nipe, 27 April 1919, *Ekman* 9572 (holotype S!, isotype NY!); near Rio Piloto, 15 Dec. 1915, *Ekman* 6670 (NY!); Manigua, near Playa

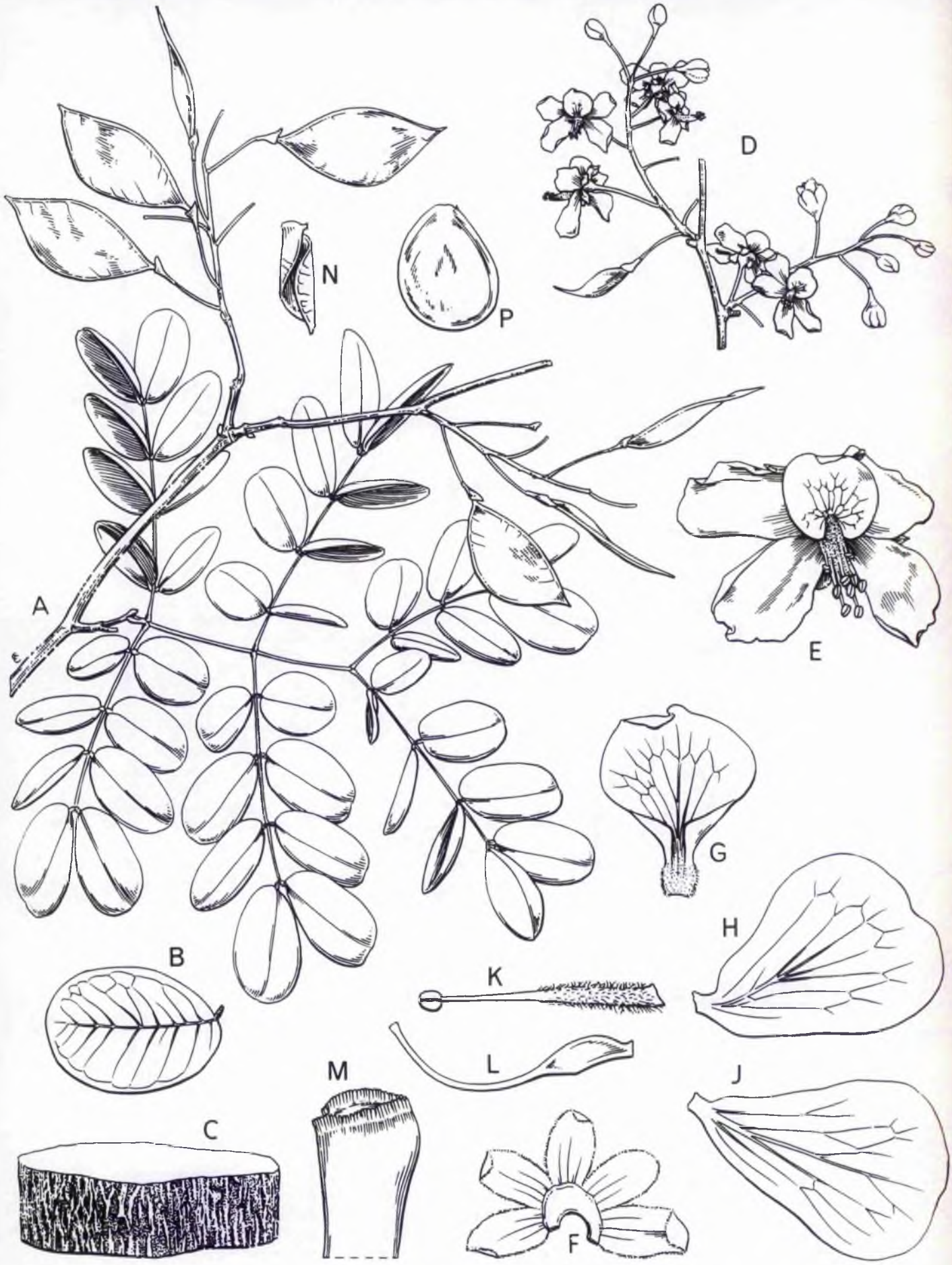


FIG. 42. *Caesalpinia nipensis*. **A** foliage and fruit x 1; **B** leaflet undersurface x 2; **C** section of branch x 1; **D** inflorescence x 1; **E** flower x 2¼; **F** calyx opened out x 3; **G** standard petal x 4½; **H** upper lateral petal x 4½; **J** lower lateral petal x 4½; **K** stamen x 4½; **L** gynoecium x 4½; **M** stigma x 45; **N** single twisted fruit valve x 1; **P** seed x 3. **A, B, N & P** from *Lewis et al.* 1842, the rest from *Lewis et al.* 1838. Drawn by Eleanor Catherine.

FIG. 43. *Caesalpinia nipensis*: **A** habitat, Cuba (*Lewis et al.* 1838); **B** bark (*Lewis et al.* 1842); **C** young fruits (*Lewis et al.* 1842); **D** flower (*Lewis et al.* 1838); **E** young shoot from subsurface stolon (*Lewis et al.* 1814); *C. myabensis*: **F** fruits (*Lewis et al.* 1845).

de Moa, 22 July 1947, *León & Clemente* 23256 (HAC!); Cayoguán, Punta Gorda, 30 March 1942, *León et al.* 20891 (HAC!); Cayoguán valley, Moa, 16 July 1947, *León & Clemente* 23113 (HAC!, US!); Rio Cayoguán, 16 July 1947, *León et al.* 5454 (HAC!); Moa valley, 22 July 1941, *León & Clemente* 20188 (HAC!, US!); Cerro de Miraflores, Cananova, July 1942, *León* 21077 (HAC!, US!); Sierra de Nipe, 6 April 1941, *León* 19854 (HAC!); Holguin province, Sierra del Cristal, just S of Levisa, 7 July 1990, *Lewis et al.* 1838 (BHU!, G!, K!, MEXU!, NY!, SI!, TEX!); Cananova, 8 July 1990, *Lewis et al.* 1842 (BHU!, G!, K!, NY!); Sierra de Nipe, Loma del Winch, 4 July 1990, *Lewis et al.* 1814 (BHU!, G!, K!, NY!); Moa, Cayo Chico, 5 May 1952, *Smith* 596 (HAC!); Moa, near Rio Yagrumajes, April 1943, *Victorin et al.* 21509 (HAC!); Moa, April 1943, *Victorin et al.* 21618 (HAC!); Moa, Rio Yagrumajes, *Victorin et al.* 21794 (HAC!); Moa, Oct. 1965, Yero 627 (HAC!); Moa, Sept. 1965, *Yero* 389 (HAC!).

ECOLOGY. Mesic charrascal scrub on serpentine rock; on scree of old nickel and cobolt mine, 40--530 m.

PHENOLOGY. Flowering February to July and also in October and November, fruiting May to August.

VERNACULAR NAME. "Cayo chiquito".

NOTES. The species has the capacity to reproduce vegetatively and young shoots arise spontaneously from subsurface stolons. Flowering is relatively sparse.

26. **Caesalpinia glandulosa** *Bertero ex DC.*, Prodr. 2: 482 (1825). Type: Hispaniola, *Bertero* 84 (holotype G-DC, n.v.).

Poincianella glandulosa (Bertero ex DC.) Britton & Rose in N. Amer. Fl. 23(5): 336 (1930).

A much-branched spiny shrub, 1.5--2 m tall, the terminal branches becoming scandent and climbing through surrounding vegetation; young stems finely puberulous with a few gland-tipped prickles intermixed, 5 mm diam. branchlets with black bark and whitish-grey pustular lenticels scattered over surface; recurved woody prickles scattered along stems with larger (3--4 mm) prickles in pairs at the nodes, a smaller pair at the insertion of each pair of pinnae or more often a cluster of prickles of diminishing size at this point, the smaller prickles gland-tipped, tiny prickles at insertion of leaflets. *Leaves* bipinnate; petiole 10--17 mm long; rhachis 2.7--5.5 cm long; pinnae in 2--4 opposite pairs, with or without an additional terminal pinna; leaflets in 5--7 pairs, terminals elliptic to obovate, 6-

-7 x 3--4.5 mm, medians narrowly oblong-elliptic to elliptic, 6--8 x 3--4.5 mm, both surfaces glabrous, only midvein visible; a few dark, punctate glands in sinuses of very slightly crenulate margin. *Inflorescence* a 10--15-flowered, pseudolateral or terminal ramiflorous raceme, the rhachis finely puberulous, prickles sometimes at peduncle base; pedicels c 8--9 mm long, articulated 0.75--1 mm below calyx. *Calyx* lobes 4.5--5 mm long, finely pubescent, margin glandular with short-stipitate pixie-cup glands, lower lobe cucullate. *Corolla* yellow (? standard with purple flecks); standard petal suborbicular-broadly ovate, 6 x 5.5--6 mm, lacking claw, outer surface densely glandular with sessile, disc-shaped glands; upper lateral petals broadly obovate to orbicular, 6 x 4.5--5.5 mm (including a 1 mm claw); lower laterals obovate, 6--7 x 3.5 mm (including a 1--1.5 mm claw), all laterals densely sessile glandular on outer surface of blade. Stamen filaments purplish, 8--9 mm long, moderately to densely pubescent on basal $^1/_2$--$^2/_3$, eglandular; anthers c 1 x 0.5 mm. Ovary densely short-pubescent with sessile glands intermixed with hairs; style c 8 mm long; stigma a terminal, tubular or funnel-shaped, fringed chamber. *Pod* coriaceous, elastically dehiscent, 5--7.5 x 1.1--1.6 cm, finely pubescent, the hairs most evident on the suture, scattered sessile and short-stipitate, reddish, pixie-cup glands on valve surface, 5--7-seeded. *Seeds* broadly ovate. (Fig. 44. Map. 15).

DISTRIBUTION. Hispaniola in both Haiti and the Dominican Republic, Cuba.

CUBA: Prov. Oriente, Costa Sur de Baracoa, Baitiquiri, 9 Feb. 1952, *Acuña & Barreto* (HAC!); Mayari, April 1957, *Acuña et al.* 20457 (HAC!); Baracoa, Imías, *Acuña* 17822 (HAC!); Meseta de Maisi, Feb. 1929, *Acuña* 16986 (HAC!); near Tortuguilla, 27 Dec. 1954, *Alain & López* 4179 (HAC!); Tortuguilla, 10 Jan. 1956, *Alain & Morton* 4961 (HAC!); Prov. Guantanamo, Imías, La Chivera, 11 April 1984, *Bisse et al.* 52775 (HAJB!); 8 km E of Imías, 12 Jan. 1956, *Morton & Alain* 8934 (US!); **HAITI**, Port-de-Paix, 3 April 1928, *Ekman* 9838 (K!); Tortue Island, near La Vallee, 4 May 1929, *Leonard & Leonard* 15332 (K!, US!); nr. Port a L'Eau, March 1929, *Leonard & Leonard* 13844 (NY!, US!); Gonaives to Plaisance, 16 Aug. 1905, *Nash & Taylor* 1768 (NY!); **DOMINICAN REPUBLIC**, Prov. Barahona, NE corner of Beata Island, 9 Aug. 1950, *Howard* 12435 (US!); Jaiquí Picado, c 20 mi. W of Santiago, 4 May 1968, *Liogier* 11088 (NY!); 9 May 1969, *Liogier* 15157 (NY!); Prov. Azua, 6 March 1980, *Mejía* 139 (NY!); between Azara & Barahona, Feb. 1971, *Votava & Liogier* 53X (NY!); Cabo Rojo, Pedernales, Feb. 1971, *Votava & Liogier* 55X (NY!).

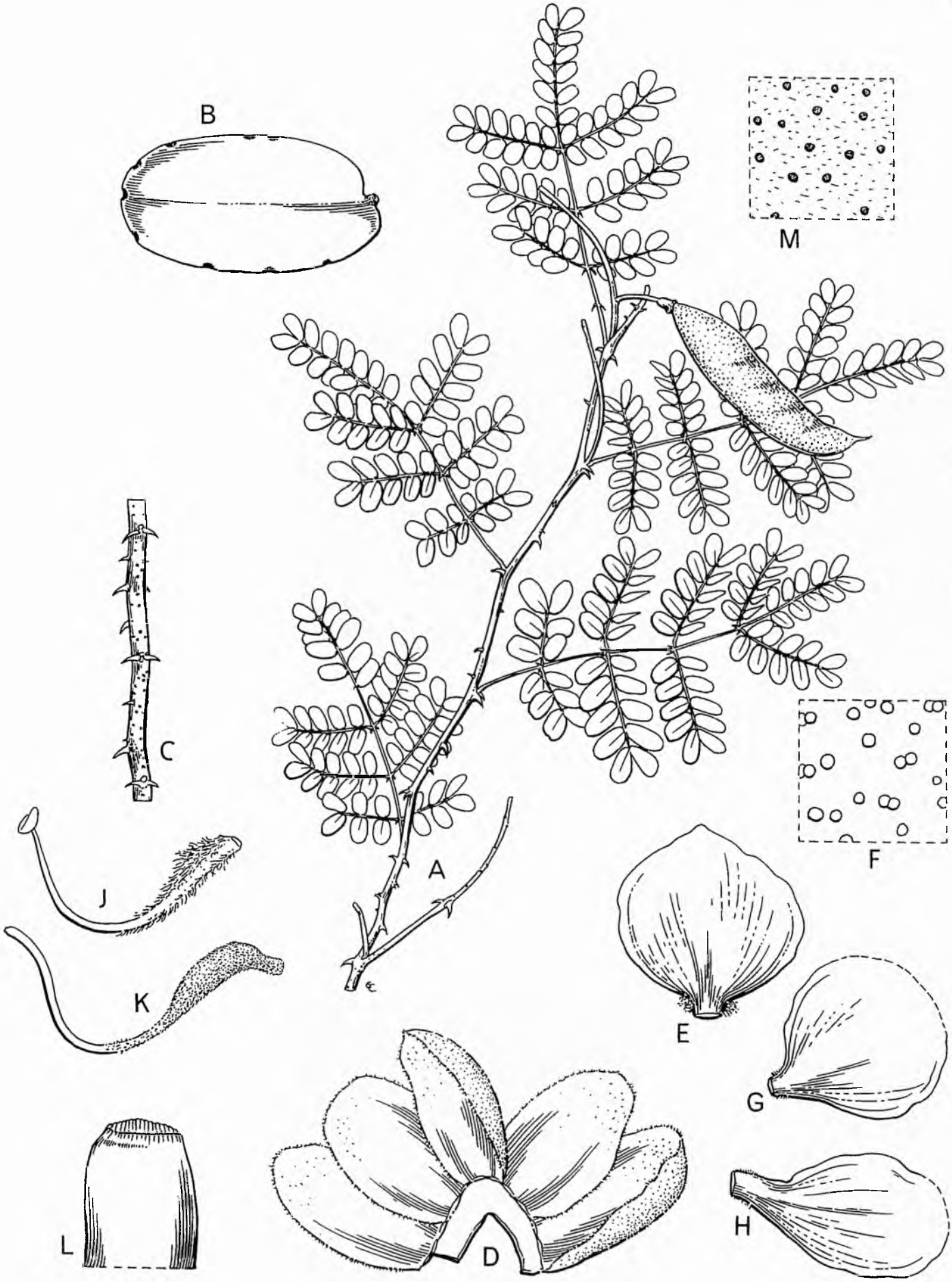


FIG. 44. *Caesalpinia glandulosa*. **A** foliage and fruit x 1; **B** leaflet undersurface x 9; **C** stem spines x 1½; **D** calyx opened out x 6; **E** standard petal x 6; **F** glands on dorsal surface of standard x 30; **G** upper lateral petal x 6; **H** lower lateral petal x 6; **J** stamen x 6; **K** gynoecium x 6; **L** stigma x 60; **M** detail of fruit surface showing glands x 15. **A** from *Leonard & Leonard* 15332, **B, C & M** from *Leonard & Leonard* 13844, **D–L** from *Votava & Liogier* 55X. Drawn by Eleanor Catherine.

ECOLOGY. Dry scrub thickets and deciduous woodland on low hills near the coast, on limestone; coastal thickets on the beach, mud flats, 0--400 m.

PHENOLOGY. Flowering from January to May (sometimes secondarily in August), fruiting from February to May (and occasionally in September).

NOTES. A highly distinctive member of the *Poincianella* group with recurved prickles and marginal punctate glands on the leaflets. It is restricted to Hispaniola and Cuba. The dorsal surfaces of all five petals are sessile-glandular and the standard petal lacks a claw, characters excluding the species from *Caesalpinia sens. strict.* Its fruits are typical *Poincianella* type and easily distinguish the species from *C. pauciflora* (a species more closely related to *Caesalpinia sens. strict.*) with which it has often been confused. (See Fig. 71).

27. **Caesalpinia marginata** *Tul.* in Arch. Mus. Paris 4: 147 (1844). Type: Bolivia, Chiquitos, near San-Juan (Bois de la Tapira), without date, *d'Orbingy* 831 (holotype P!).

Cenostigma sclerophyllum Malme in Bih. Svensk. Vet.-Akad. Handl. 25 (11): 24 (1900). Type: Paraguay, Colonia Risso, near Rio Apa, 20 Oct. 1893, *Malme* 1084 (lectotype S!, chosen here, isolectotype S!).

Unarmed shrub, 1--2 m tall; older stems glabrous, young stems with a dense, short, white pubescence or glabrous. *Leaves* pinnate; petiole 1--15 mm long (the leaf sometimes almost sessile); rhachis 1.2--10 cm long; leaflets sessile, coriaceous, in (1--)2--4 opposite to alternate pairs, becoming progressively larger towards distal end of leaf rhachis, terminal leaflets obliquely obovate, 5--7.5 x 3--4.5 cm, median leaflets obliquely obovate, obovate-elliptic or suborbicular, 3.7--6.4 x 2.2--4.2 cm, both surfaces of all leaflets glabrous, secondary venation brochidodromous, the loops forming a prominent marginal or submarginal vein, secondary and tertiary venation prominent on both surfaces, often drying a different colour to the blade on the upper surface; sessile, disc or dome-shaped glands scattered along margin of leaflet. *Inflorescence* an axillary or terminal raceme of c 13--21 flowers; peduncle and pedicels densely pubescent; bracts ovate-lanceolate; pedicels 10--14 mm long, articulated exactly at, just above or just below the middle. *Calyx* lower

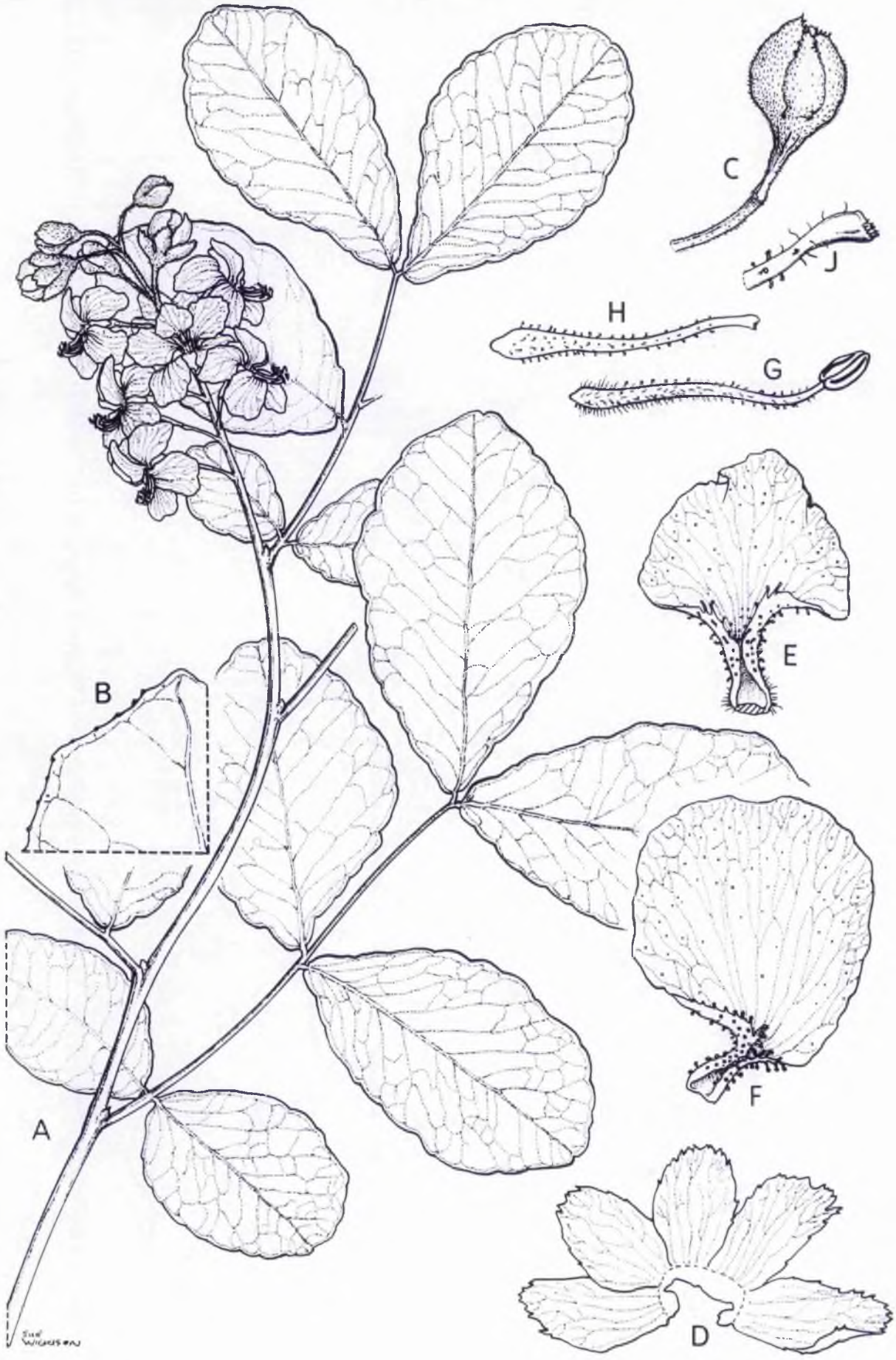


FIG. 45. *Caesalpinia marginata*. **A** inflorescence and foliage x 1; **B** detail of leaflet margin showing glands x 1; **C** bud and pedicel showing position of articulation x 3; **D** calyx opened out x 3; **E** standard petal x 4½; **F** lateral petal x 4½; **G** stamen x 4½; **H** gynoecium x 4½; **J** stigma x 9. All from *Pott et al.* 4600. Drawn by Sue Wickison.

lobe ± cucullate, slightly longer than the other four which are 4.5--9 mm long, all lobes tomentulose, especially on the inner surface, apices fimbriate; subepidermal, orbicular or oblong glands scattered over sepal surfaces. *Corolla* yellow; subepidermal glands scattered over petal blade surfaces; standard petal blade broadly triangular to suborbicular, 10 x 7--7.5 mm (including a 3 mm claw), the claw thickened, it and lower ½ of dorsal surface of blade glandular with stalked pixie-cup glands; upper lateral petals with obliquely obovate-

elliptic blade,13 x 7.5--8 mm (including a 2 mm claw), claw thickened and glandular with short-stalked pixie-cup glands; lower lateral petals with oblong-obovate blade, 12.5--14 x 5--7.5 mm (including a 3 mm claw). Stamen filaments 9--11 mm long, pubescent on lower $^1/_2$--$^2/_3$, glandular along entire length with short-stalked pixie-cups glands; anthers 2 x 1--1.25 mm, the thecae, especially near the apex occasionally with small subepidermal glands (as on the petal blades). Ovary puberulous with sessile glands intermixed; style 7--8 mm long; stigma a terminal, bulbous, fringed chamber. *Fruit* a thinly woody, dehiscent pod, 5.2 x 1.9 cm (including a 2 mm stipe), glabrous, eglandular, 1--3-seeded. (Fig. **45**, Map 22).

DISTRIBUTION. Bolivia, western Brazil, northern Paraguay.

BRAZIL. Mato Grosso do Sul, Mun. Porto Murtinho, 18 km W of corrego Capivara, 17 Feb. 1989, *Pott el al.* 4600 (K!); **BOLIVIA.** Depto. Santa Cruz, near Roboré, 29 Sept. 1928, *Bourke-Borrowes* 67 (K!); Prov. Chiquitos, 2 km W of Aguas Calientes, 23 Nov. 1989, *Nee* 37870 (K!); Chiquitos, without date, *d'Orbigny* 831 (holotype P!); **PARAGUAY** between Rio Apa and Rio Aquidaban, 1908--1909, *Fiebrig* 5219 (K!); Chaco, Cerro León (Cap. Pablo Lagerenza), NE de ex Misión Nueva Tribu, 29 Oct. 1987, *Spichiger et al.* 557 (RS2603) (G!).

ECOLOGY. Subtropical semi deciduous forest, on sand or sandy loam; by hot springs; on poorly drained sedimentary soil of savanna chaquenha, 100--300 m.

PHENOLOGY. Poorly-known, probably flowering from September to February and fruiting November to March.

28. **Caesalpinia pyramidalis** *Tul.* in Archiv. Mus. Paris 4: 139 (1844). Type: Brazil, Jacobina, 1841, *Blanchet* 3425 (holotype P, n.v., isotypes BM!, BR!, F!, MG!).

Unarmed shrub to multiple-trunked small tree, 1--6 m tall, DBH of main trunks 8--35 cm; bark smooth, whitish grey or dark brown; stems sparsely pubescent to glabrous. *Leaves* bipinnate; stipules linear-spathulate to broadly spathulate, c 4--5 x 3 mm reticulately veined, glandular, glabrous, persistent; petiole 1.5--2.4 cm, pubescent or glabrous, eglandular or sparsely glandular; rhachis 0--5.8 cm long, pubescent or glabrescent, moderately glandular; pinnae in 1--3 opposite pairs plus a terminal pinna (or this lacking and leaf ending in a terminal pair), the pinnae rhachides pubescent; leaflets 3--11 per pinna, alternate or the terminal two opposite and sometimes much longer than the proximal ones, subrhombic, subquadrate, suborbicular or broadly ovate to ovate-elliptic, the margin undulate, terminal leaflets 1.8--5.6 x 1.1--3.3 cm, medians 1.5--3.6 x 1--3 cm, upper surface sparsely pubescent or glabrous, sometimes ± nitid, lower surface glabrous, venation prominent on both surfaces, secondary veins brochidodromous; juvenile leaflets and leaf rhachides are sometimes densely glandular with stipitate, pixie-cup glands, these with pubescent stalks, some mature leaflets with subepidermal glands evident on the lower surface or along the undulate or shallowly crenulate margin, some break the leaflet surface as sessile, secretory glands. *Inflorescences* multi-flowered, terminal, pyramidal racemes, these sometimes aggregated into a few-branched panicle; rhachis, pedicels and calyces greyish yellow or rusty-brown tomentose, eglandular, plumose hairs sometimes on very young inflorescence branches and older pedicels, after flower fall the rhachis persisting as a knobbly axis; bracts ovate-lanceolate, acute to acuminate, c 3--6 mm long, densely tomentose, occasionally with subepidermal glands in blades, caducous or subpersistent to ± flower anthesis; pedicels (7--)13--19 mm long, articulated 1--12 mm below base of calyx, after flower abortion the lower part of the pedicel sometimes persisting. *Calyx* lobes 5--8 mm long, the lowest, cucullate lobe 7--11 mm long, both lobe surfaces tomentose, subepidermal idioblasts in blades, apices fimbriate. *Corolla* yellow, the standard with a network of orangish red veins, blade ovate-elliptic (spathulate if claw included), 8--12 x 5--7 mm (including a 3--4 mm claw), claw inner surface thickened and grooved, apex with a thickened, glandular or sometimes densely pubescent ridge; upper lateral petals broadly elliptic to suborbicular, 10.5--13 x 8--10 mm (including a 2--4 mm

claw, this somewhat bent to one side); lower laterals elliptic to subrectangular, 11--14 x 7--8 mm (including a 1.5--3 mm claw, sometimes ± bent to one side); all 5 petals with blade and claw glandular on the dorsal surface (sometimes only lower portion of blade glandular) and with subepidermal glands in blades, the 4 lateral petals with the claw margins pubescent and stipitate-glandular, the inner surfaces moderately to densely pubescent. Stamen filaments 13--17 mm long, pubescent on the basal $^1/_2$ (densely so on the basal $^1/_4$--$^1/_3$), some filaments of each flower with the inner surface sparsely to moderately stipitate-glandular; anthers 1.5 x 1 mm, the thecae sparsely glandular, the thickened thecal bridge with a dark gland. Ovary densely pubescent with short-stalked glands intermixed or the glands hidden by the indumentum, 6--7(--8)-ovulate; style c 9 mm long, pubescent and glandular, thickened at apex; stigma a terminal, fringed chamber. *Fruit* a woody, explosively dehiscent, 4--6-seeded pod, 8.5--14 x
(1.7--)1.8--3 cm (including a 3 mm stipe and 4 mm beak), the upper margin thicker than the lower one, the valves moderately pubescent, glabrescent, the hairs most evident on the suture.

28a. var. **pyramidalis**

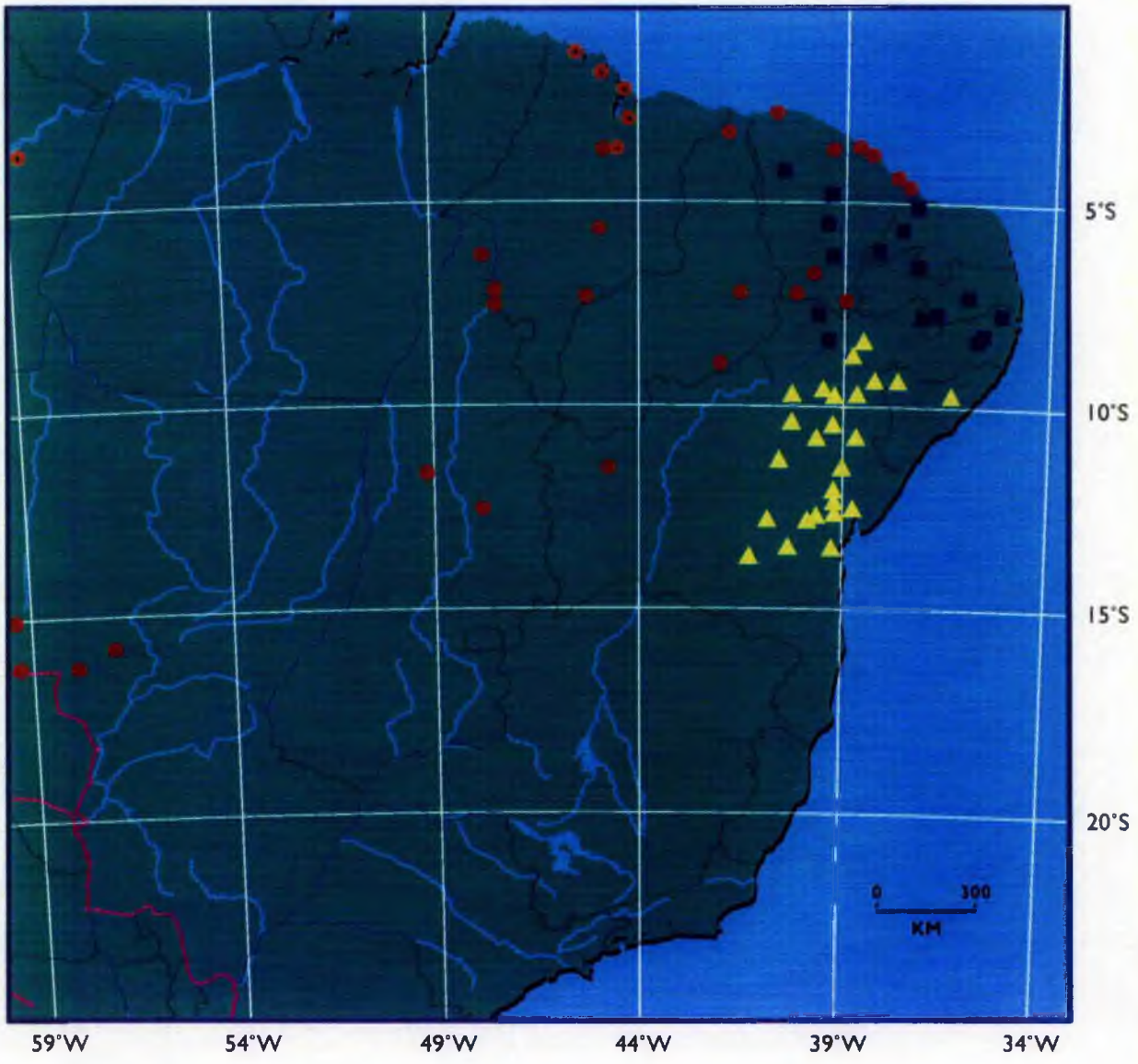
Caesalpinia pyramidalis Tul. var. *alagoensis* Tul. in Archiv. Mus. Paris 4: 140 (1844). Type: Brazil, Alagoas, banks of the Rio St. Francisco at Propiá, Feb. 1838, *Gardner* 1278 (holotype BM!, isotypes F!, GH!, K!, US!).

Pedicels articulated 10--12 mm below calyx (i.e. well below its middle), bracts 3--3.5 mm long, standard claw apex with a glandular ridge, inflorescence indumentum greyish yellow, terminal leaflets 1.8--4.2 cm long. (Map 16).

DISTRIBUTION. Brazil in the states of Pernambuco, Alagoas and Bahia.

BRAZIL: Pernambuco, Mun. de Floresta, BR-316, 6 km from Floresta, 30 May 1984, *Almeida & Ferreira* 304 (RB!); without exact locality, 26 Nov. 1978, *Leitão Filho & Timoni* 8909 (MBM!, MG!, RB!, UEC!); **Alagoas**, banks of Rio St. Francisco, Feb. 1838, *Gardner* 1278 (BM!, F!, GH!, K!, US!); c 10 km E of Arapiraca, 30 Jan. 1982, *Kirkbride* 4601 (NY!); **Bahia**, Feira de Santana, 10 Oct. 1978, *Araújo* 069 (F!); 220 km S of Salvador, 28 Jan. 1965, *Belém & Mendes* 315 (NY!, UB!); Jacobina, 1841. *Blanchet* 3425 (holotype P, isotypes BR!, F!, MG!); Jacobina, *Blanchet* 3669 (BR!, F!, MG!); Mun. de Tucano, 7 km

Distribution of *Caesalpinia bracteosa* (●) *C. gardneriana* (■) *C. pyramidalis* var. *pyramidalis* (△) and *C. pyramidalis* var. *diversifolia* (◍) in Brazil



along road from Tucano to Araci, 28 Feb. 1992, *Carvalho & Hind* 3828 (K!); 2 March 1992, *Carvalho & Hind* 3879 (K!); Mun. de Conceição de Feira, 17 Feb. 1981, *Carvalho et al.* 542 (K!); Mina Caraiba, 17 March 1966, *Castellanos* 25811 (K!, M!); 7 km N of Formosa, 17 July 1964, *Castellanos* 25152 (F!); Mun. Juazeiro, road BR-407 from Juazeiro to Senhor do Bonfim, 25 June 1983, *Coradin et al.* 5990 (K!, NY!); 25 June 1983, *Coradin et al.* 6016 (K!); Juimazones, 7 May 1918, *Curran* 131 (F!, GH!, US!); c 21 km SW of Tanquinho, 31 March 1976, *Davidse et al.* 11673 (US!); 7 km from Formosa on the BR-13, 17 July 1964, *Duarte & Castellanos* 427 (NY!); Mun. de Glória, c 35 km S of Barra do Tarrachil on road to Canudos, 17 July 1962, *Eiten & Eiten* 4970 (US!); Ituaçú, Morro da Mangabeira, 22 Dec. 1983, *Gouvêia* 66/83 (K!); SW of Monte Santo by Rio Cariaçã, 21 Feb. 1974, *Harley et al.* 16446 (K!); 6 km E of Itiuba, 19 Feb. 1974, *Harley et al.* 16188 (K!); near Milagres, 18 July 1979, *Hatschbach & Guimares* 42457 (HBG!); Tanque Novo, Nov. 1913--Feb. 1914, *Luetzelburg* 734 (M!); without exact locality, without date, *Martius* s.n. (Obsv. 2232) (M!); Mun. de Itaetê, km 29 on road Itaetê to Marcionillo Dias, 23 May 1989, *Mattos Silva et al.* 2847 (K!); Mun. de Paulo Afonso, Vila Nobre, 6 June 1981, *Mori & Boom* 14207 (K!, US!); Paulo Afonso, 6 June 1981, *Mori & Boom* 14200 (K!, US!); Feira de Santana, Serra de São José, 1 March 1985, *Noblick & Lemos* 3545 (K!); Cachoeira, road to Rio Jacuípe, April 1980, *Groupo Pedra do Cavalo* 2 (K!); between Maracás and Tambaré, 24 Jan. 1965, *Pereira* 9725 & *Pabst* 8614 (F!, K!, M!, NY!); Queimada, 25 July 1951, *Pires* 3442 (NY!); Mun. de Anguera, c 6 km W of entrance to Serra Preta, 30 Nov. 1991, *Queiroz* 2518 (K!); 30 km N of Serrinha, 2 Nov. 1972, *Ratter et al.* R2708 (E!, K!), R2708A (UB!); 2 Nov. 1972, *Ratter & Fonsêca* R2707 (E!, K!); Queimadas, 9--11 June 1915, *Rose & Russell* 19841 (NY!, US!); Rodelas, 20 Jan. 1987, *Silva & Silva* 26 (CEPEC!); Mun. Uauá, 1.7 km ESE of Uauá towards Canudos, 6 Jan. 1991, *Taylor et al.* 1361 (BR!, K!, MEXU!, NY!, Z!); Uauá, Carataca, 3 Nov. 1978, *Walmor* 005 (F!).

ECOLOGY. Caatinga, especially on elevated, rocky places; mata de galeria (a single record), 350--750 m.

PHENOLOGY. Flowering and fruiting from November to July and occasionally in September and October.

VERNACULAR NAMES. "Caatingueira", "caatingueira alta", "catinga de porco", "pau de rato", "mussitáiba" (Bahia).

NOTES. *C. pyramidalis* var. *pyramidalis* is one of the commonest shrubs of secondary caatinga and is easily distinguished from var. *diversifolia* and other related taxa by its pedicels which are articulated well below the mid point. Even on the lignified pedicel of a mature fruit this articulation point remains very evident.

A tea made from the flowers is used to cure colds (*Silva & Silva* 26); *Pires* 3442 reports that the foliage has an adverse effect on cattle.

28b. var. **diversifolia** Benth. in Mart. Fl. Bras. 15(2): 69 (1870). Type: Brazil, Maranhão, June 1841, *Gardner* 6006 (lectotype K!, chosen here, isolectotype BM!).

Pedicels articulated 1--4.5 mm below calyx (i.e. above middle), bracts 4.5--6 mm long, standard claw apex with a densely pubescent ridge, inflorescence indumentum rusty brown, terminal leaflets 4--5.6 cm long. (Map 16).

DISTRIBUTION. Brazil in the states of Amazonas, Maranhão and Ceará.

BRAZIL: Amazonas, Prov. Rio Negro, Barra do Rio Negro [Manaus], without date, *Martius* s.n. (M!); **Maranhão**, Perizes, 7 July 1954, *Black et al.* 54--16457 (GH!, INPA!); Alcântara, 4 Feb. 1984, *de Carvalho et al.* 2081 (K!); c 15--30 km N of São Mateus, 28 Sept. 1980, *Daly* D345 (K!, NY!, US!); Maracassumé River Region, Ilha do Trauira, 29 Aug. 1932, *Froes* 1824 (F!, K!, NY!); without exact locality, June 1841, *Gardner* 6006 (lectotype K!, isolectotype BM!); Cururupú, fazenda Rosario, Aug. 1914, *Lisbôa* 53 (K!); Santa Elena, 9 July 1978, *Rosa & Cardos* 2561 (MG!, NY!, UEC!); **Ceará**, without exact locality, Oct. 1922, *Rondon* s.n. (RB. No. 17019) (RB!).

ECOLOGY. Campo on high rocky ground.

PHENOLOGY. Flowering from June to October (with one record for February), poorly known in fruit but collected in February and July.

VERNACULAR NAME. "Campeche" (Maranhão).

NOTES. The species is easily confused with *C. bracteosa* in the absence of flowers which are larger in the latter, aggregated into panicles and have much larger floral bracts.

29. **Caesalpinia bracteosa** *Tul.* in Archiv. Mus. Paris 4: 141 (1844). Type: Brazil, Piauí, *Gardner* 2144 (holotype P, n.v., isotypes BM!, K!).

Unarmed shrub or small tree, 1--6(--15) m tall, DBH 15--60 cm; bark pale grey or pale brownish-grey; stems pubescent or glabrous. *Leaves* bipinnate; stipules caducous; petiole 1--4.5 cm long, pubescent or glabrous, glandular; rhachis 2.7--4.8 cm long, pubescent or glabrous, glandular with scattered, squat glands (head width = stalk length) or eglandular; pinnae in 1--3 alternate to opposite pairs plus a terminal pinna (or this

lacking and leaf ending in a pair of pinnae), each pinna terminating in a small mucro; leaflets sessile, 5--13 per pinna, alternate, the distal ones larger than the proximal ones or the medians larger than the rest, coriaceous, malodorous, oblong-elliptic, broadly ovate or ovate-rhombic, terminal leaflets 3.3--8 x 1.3--4.3 cm, medians 2.3--5.5 x 1.5--4 cm, apex rounded to obtuse, or acute and mucronulate, base truncate, both surfaces glabrous or pubescent; venation prominent on both surfaces or only on lower surface, main vein oblique, secondary veins brochidodromous, tertiary veins reticulate, leaflet blades with scattered, dark, subepidermal glands, margin glandular with regularly spaced, sessile (not punctate) glands. *Inflorescence* a terminal panicle, the rhachis, pedicels and calyces densely rusty or golden brown tomentose, some hairs plumose or ± stellate, panicles up to 12-branched with each branch (raceme) 10--60-flowered, a pedicel ridge prominent after flower fall, the rhachis appearing as a small backbone; bracts broadly ovate, acute, 8--12 mm long, densely tomentose, margin ± fimbriate, persisting at apex until bud expansion, then caducous; pedicels 8--12 mm long, articulated directly below calyx. *Calyx* lobes elliptic, apex rounded, 7--9 mm long, lowest lobe 9--11 mm long, all lobes with both surfaces densely tomentose or the inner surface lanate, a few subepidermal glands scattered in sepal blades. *Corolla* bright yellow; standard petal slightly speckled orange, blade suborbicular to broadly obovate (panduriform if claw included), 13--15 x 9--10 mm (including a 4--6 mm claw), outer surface of blade stipitate-glandular, subepidermal glands in blade, claw thickened, outer surface and margins stipitate-glandular, inner surface sparsely pubescent, claw apex with a membranous cocks-comb ridge on either side of a central groove; upper lateral petals broadly ovate-orbicular, 15--17 x 14 mm (including a 3--4 mm claw), lower laterals subrectangular-elliptic, 16--17 x 11--13 mm (including a 2--3 mm claw), all laterals with ragged or indented apices, subepidermal dot-dash glands in blades, base of blade infolded and thickened claws bent at right angles to vertical plane of blade, claws densely lanate and glandular-margined, outer surface of upper lateral claws glandular. Stamen filaments 18--21 mm long, basal ½ densely pubescent, upper ½ thinly so, inner face of some filaments sparsely to moderately stipitate-glandular; anthers 2 x 1 mm, with dark idioblast in thickened thecal bridge, or this apparently lacking. Ovary densely pubescent; style basal $^1/_3$--$^1/_2$ moderately pubescent with short-stalked glands intermixed; stigma a slightly gibbous, terminal, fringed chamber. *Fruit* a reticulately veined, woody, explosively dehiscent 5--6-seeded pod, 8--14 x 2--2.7 cm (including a 5

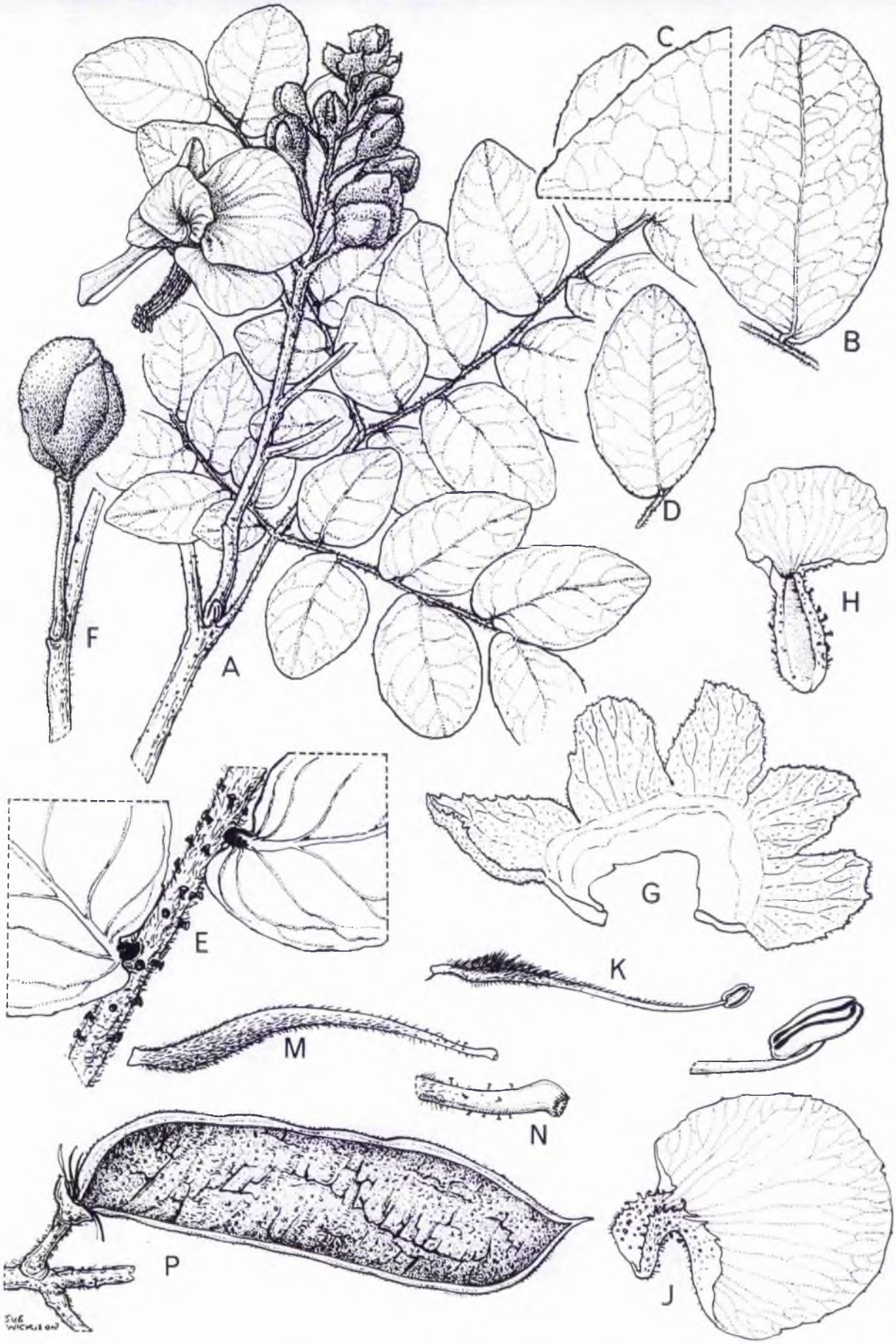


FIG. 46. *Caesalpinia bracteosa*. **A** inflorescence and bipinnate leaf x 1; **B** leaflet upper surface x 1; **C** detail of glandular leaflet margin x 4½; **D** leaflet undersurface x 1; **E** glandular pinna rhachis and leaflet insertions x 4½; **F** bud x 3; **G** calyx opened out x 3; **H** standard petal x 3; **J** upper lateral petal x 3; **K** stamen x 3; **L** anther x 9; **M** gynoecium x 3; **N** stigma x 9; **P** fruit x 1. **A**, **D–N** from *Lewis & Pearson* 1149, **B** & **C** from *Gardner* 2146, **P** from *Duarte* 465 & *Castellanos*. Drawn by Sue Wickison.

mm beak); upper margin more strongly ridged than lower one, valves very finely puberulous, glabrescent, eglandular or glandular with scattered, sessile or short-stalked glands. *Seeds* quadrate-orbicular, 12 x 11 x 2 mm. (Figs. **46** & 48A & B, Map 16).

DISTRIBUTION. Brazil in the states of Maranhão, Piauí, Ceará, Bahia, Goiás and Mato Grosso.

BRAZIL: Maranhão. Mun. de Lorêto, "Ilha de Balsas", c 40 km S of Lorêto, 29 March 1962, *Eiten & Eiten* 3935 (K!, NY!); same locality, 25 Feb. 1970, *Eiten & Eiten* 10782 (K!, NY!, UB!); c 40 km S of Lorêto, 27 March 1962, *Eiten & Eiten* 3896 (NY!); nr. Coroatasinho, 24 March 1933, *Krukoff* 2045 (K!); Mun. Carolina, 9 Aug. 1955, *Macêdo* 4006 (RB!, US!); Mun. de Tuntum, Palmerinha, 74 km from Tuntum, 27 Feb. 1983, *Santos et al.* 692 (F!, K!, NY!); **Piauí**, Picos to Oeiras, 30 July 1964, *Castellanos & Duarte* 575 (NY!); banks of the Rio Caminde, May 1839, *Gardner* 2144 (holotype P, isotype K!); Boa Esperança, March 1839, *Gardner* 2146 (K!); Mun. de Raimundo Nonato, c 8 km from the Fundação Ruralista on road to Vitorino, 17 Jan. 1982, *Lewis & Pearson* 1099 (K!); c 5 km N of Fundação Ruralista, 21 Jan. 1982, *Lewis & Pearson* 1149 (K!); 17 Jan. 1982, *Lewis & Pearson* 1095 (K!); Fundação Ruralista, 28 Nov. 1981, *Pearson* 44 (K!); **Ceará**, 87 km W of Fortaleza, 6 km E of Riachão de Sella, 6 July 1944, *Cutler* 8123 (F!); nr. Assaré, 29 Aug. 1945, *Cutler* 8411 (F!); Mun. Fortaleza, nr. Rio Maranguapinho, 2 km S of Porangaba, 24 Aug. 1935, *Drouet* 2344 (F!, NY!); 20 km from Brejo Santo, 19 July 1964, *Duarte 465 & Castellanos* (NY!); nr. Aracati, July 1838, *Gardner* 1577 (K!); 21 km SW of Potenji on CE-090, 15 Feb. 1985, *Gentry et al.* 50130 (K!, NY!); Majorlândia, 10 km E of Aracati, 18 Jan. 1972, *Johnson* 13 (NY!); Mun. de Pacatuba, Sítio do Pitaguarí, 27 July 1979, *de Paula & Mendonça* 1288 (K!); 2°57'S, 40°56'W, 3 Aug. 1978, *Sakpoo* 41 (K!); **Bahia**, Mun. Riacho das Neves, road from Barreiras to Corrente, km 73, 16 June 1983, *Coradin et al.* 5738 (K!, NY!); exact locality equivocal, 7 May 1918, *Curran* 131 (GH!); without exact locality, without date, *Martius* s.n. (Obsv. 2425) (M!); **Goiás**, Mun. Gurupi, Rio Sta. Tereza, 25 March 1976, *Hatschbach & Kummrow* 38330 (MBM!, NY!, UEC!); Mun. de Tocantinópolis, 26 March 1983, *Miranda & Arouck Ferreira* 391 (RB!); W bank of Rio Tocantins, 8 km N of Filadélfia, 4 Aug. 1964, *Prance & Silva* 58556 (K!, UB!); **Mato Grosso**, Vila Bela, km 12 on road to Fazenda Formosa, 8 May 1983, *Carreira et al.* 940 (NY!); km 134 on road Cáceres to S of Serra do Aguapei, 4 March 1977, *Kirkbride & Lleras* 3073 (BR!, F!, INPA!, K!, NY!, US!); Cuiabá to Cáceres highway, 12 Feb. 1980, *Macedo et al.* 1496 (NY!).

ECOLOGY. Caatinga on sandy soil, cerradão, mesophytic gallery forest, campo cerrado and coastal dunes, 100--620 m.

PHENOLOGY. Flowering from November to July, fruiting from early January to August.

VERNACULAR NAMES. "Pau de rato" (Maranhão and Piauí), "Catingueira" (Ceará).

NOTES. *Prance and Silva* 58556 recorded that the plant is used locally in northern Goiás as a cure for dysentery.

The species has been frequently misidentified and confused with *C. pyramidalis* and *C. gardneriana* but it differs from both by its much larger flowers and large, semi persistent floral bracts. It is very similar to *C. pyramidalis* var. *diversifolia* which is, in some instances, only separable by its smaller, lanceolate, acute to acuminate floral bracts and racemose inflorescences.

Specimens from Maranhão tend to be taller trees, attaining 15 metres in height.

30. **Caesalpinia gardneriana** *Benth.* in Mart. Fl. Bras. 15(2): 68 (1870). Type: Brazil, Piauí, between Praya Grande and Boa Esperança, Feb. 1839, *Gardner* 2148 (holotype K!, isotype BM!).

Unarmed shrub to small tree, 3--8(--12) m tall, DBH 15--25 cm; bark smooth, pale grey; stems with white pustular lenticels, very sparsely pubescent, glabrescent. *Leaves* bipinnate; stipules early caducous; petiole 1.8--2.3 cm long, pubescent, eglandular or with a few to many scattered glands intermixed with the indumentum; rhachis 1.7--2.5 cm long, as for petiole; pinnae in 1--2(--3) subopposite pairs plus a terminal pinna; leaflets 6--10 per pinna, alternate, rhombic to suborbicular or subrectangular (variable in shape on one branchlet), terminal leaflets 1.7--4.2 x 1--3.3 cm, medians 1.4--2.7 x 1.1--2.2 cm, both surfaces sparsely puberulous to pubescent; main vein oblique, secondary veins brochidodromous; leaflet blades eglandular or with scattered surface glands and subepidermal glands, sometimes densely stipitate-glandular, margins with sessile glands. *Inflorescence* a multi-flowered, terminal or leaf-opposed compact panicle, rhachis, pedicels and calyces rusty brown or yellowish brown tomentose, stellate hairs intermixed with the simple hairs and sometimes dense; bracts ovate-lanceolate, acute to acuminate, 2.5--4 mm long, densely tomentose, sometimes a few subepidermal glands in the apex, caducous; pedicels 5--9(--12) mm long, slender (under 0.5 mm wide), articulated just below to 2 mm below calyx. *Calyx* lobes 4.5--6 mm long, lowest one cucullate, 7--8 mm long, all

tomentose. *Corolla* golden yellow; standard petal with reddish spots, blade suborbicular to broadly ovate, 7.5--10 x 6--7 mm (including a 2.5--3 mm claw), dorsal surface of blade and claw stipitate-glandular, claw margin pubescent, inner surface thickened, vertically ridged, apex with shallow eglandular or glandular, pubescent flanges; upper lateral petals suborbicular, 9--11 x 8 mm (including a 2--2.5 mm claw), blade base upturned, claw bent at right angles to vertical plane of blade, lower laterals obovate to subrectangular, 11--12 x 7--8 mm (including a 1.5--2.5 mm claw), all laterals with dorsal surface of blade and claw stipitate-glandular and subepidermal glands in upper ½ of blade (these sometimes sparse), base of blade on inner face sparsely pubescent, claw margins stipitate-glandular and pubescent, inner surface pubescent. Stamen filaments (8--)10--14 mm long, pubescent especially on basal ½, some filaments stipitate-glandular on upper surface for entire length; anthers 1 x 0.5 mm, the thecae glandular and a gland in the expanded thecal bridge. Ovary densely pubescent with short, patent hairs with a few sessile or stalked glands intermixed, stigma a thickened, terminal, fringed chamber. *Pod* woody, explosively dehiscent, 7.5--8.7 x 1.7--2.2 cm (including a 4 mm stipe and 8 mm beak), valves sparsely pubescent, the hairs most obvious on the suture, 3--5-seeded. *Seeds* broadly ovate, 11 x 10 x 2 mm, brown, shiny. (Map 16).

DISTRIBUTION. Brazil in the states of Piauí, Ceará, Rio Grande do Norte, Paraiba and Pernambuco.

BRAZIL: Piauí, between Praya Grande and Boa Esperança, Feb. 1839, *Gardner* 2148 (holotype K!); **Ceará**, Sta. Cruz, 1935, *Dahlgren* 923 (F!); Mun. de Senador Pompeu, road Senador to Solonópole, 22 May 1984, *Jordy Filho* 186 (RB!); Quixadá, 24 May 1979, *Miranda* 320 (F!); Iguatú, sitio Virtude, 20 Jan. 1965, *Silva* 329 (UB!); **Rio Grande do Norte**, Mun. de Caraubas, road Caraubas to Olho d'Agua dos Borges, 1 June 1984, *Collares & Dutra* 144 (NY!, RB!); Serra Borborema, *Luetzelburg* 12476 (M!); Baraunas, 18 Feb. 1978, *Odilon* 002 (RB!); Mun. de Pau dos Ferros, Fazenda Torrão, 14 May 1984, *de Assis & Sarmento* 375 (K!); road between Mossoró and Limoeiro do Norte, 20 July 1961, *Tavares* 691 (US!); **Paraiba**, Esperança, Lagoa de Pedra, 30 Nov. 1980, *Fevereiro & Mayo* 714 (K!); Alagra do Monteiro, Serra Jabitacá, Nov. 1920, *Luetzelburg* 12026 (M!, NY!); São Gonçalo, 16 April 1936, *Luetzelburg* 28024 (M!, NY!); São Gonçalo, 30 Jan. 1936, *Luetzelburg* 26827 (F!, K!, M!); Mun. de Campina Grande, 16 Jan. 1970, *Souto et al.* 20 (NY!); **Pernambuco**, Cabrobó, BR-316 c 7 km in direction of Ibó, 12 March 1982, *Cavalcanti et al.* CFPE 231 (F!); nr. Caruaru, 25 Sept. 1976, *Davis & Andrade-Lima* D 61141 (E!); Mun. de Bodocó, 28 km SE of Ouricuri, 7 March 1970, *Eiten & Eiten* 10860 (K!, NY!); road Recife to Pesqueira, 21 Feb. 1962, *Gomes et*

al. 1240 (RB!); Caruari, 4 Nov. 1931, *Pickel* 2831 (F!, GH!); without exact locality, without date, *Sobrinho* 356 (F!); Serra do Genipapo, Bello Jardim, 14--15 Nov. 1924, *Chase* 7690 (NY!).

ECOLOGY. Caatinga, 150--600 m.

PHENOLOGY. Flowering from November to July and occasionally in September, fruiting January to July and into September.

VERNACULAR NAMES. "Catingueira" (most areas), "Catinga de porco" (Paraiba), "Catingueira da folha miuda" (Ceará).

NOTES. *Jordy Filho* 186 reports a large number of uses for the species including construction timber, fence posts, forage and charcoal.

Some specimens from Pernambuco have characters which intergrade with those of *C. laxiflora* from further south. The species appears as a diminuitive form of *C. bracteosa* with smaller flowers, leaves and, especially, floral bracts. It shares the paniculate inflorescences and pedicels articulated directly below the calyx. Except in leaflet shape, size and leaf formula *C. gardneriana* seems closely related to the widespread *C. pluviosa*. This relationship needs to be studied in more detail.

31. **Caesalpinia laxiflora** *Tul.* in Archiv. Mus. Paris 4: 143 (1844). Type: Brazil, Bahia, near Villa da Barra, *Blanchet* 3146 (holotype P, n.v., isotypes BM!, BR!, F!, GH!, K!, MG!).

Caesalpinia laxiflora Tul. var. *pubescens* Benth. in Mart. Fl. Bras. 15(2): 70 (1870). Type: Brazil, Bahia, near Maracás, *Martius* s.n. (holotype M!, isotypes M!).

Unarmed shrub, contorted multiple-stemmed treelet or small compact tree, 0.75--6 m tall, main stems 2--12 cm in diam.; bark grey, brown or mottled shades of grey and white, smooth; stems glabrous or pubescent, sparsely stipitate-glandular. *Leaves* bipinnate; stipules linear, 5 x 0.75 mm, surface with subepidermal idioblasts, outer surface with squat, ± stellate or plumose hairs and/or stipitate-glandular, the gland stalks hairy, margins ciliate, fimbriate, the fimbriae gland-tipped, early caducous; petiole 2.8--4.8(--6) cm long, glabrous or pubescent, sparsely to densely stipitate-glandular; rhachis 3.5--4(--

10) cm long, glabrous or pubescent, sparsely to densely stipitate-glandular; pinnae in 1--3 opposite to alternate pairs, plus a terminal pinna, or this lacking, pinnae rhachides sometimes pubescent along upper edge; leaflets semi coriaceous, (2--)3--9(--11) per pinna, alternate (rarely opposite on terminal pinna), broadly ovate to suborbicular, apex rounded, base shallowly cordate, strongly asymmetric, terminal leaflets (1.8--)2--7.5 x (1.2--)1.4--7 cm, medians (1.4--)1.5--6 x (1--)1.6--6 cm, margins often crinkled-wavy, both surfaces glabrous or pubescent, the margins sometimes ciliate; venation prominent on both surfaces, usually 5--7 secondary veins arising from leaflet base, then brochidodromous, tertiary venation finely reticulate; blades eglandular or sparsely to densely glandular on lower surface with widely scattered, short-stalked or sessile, discoid or globose glands (these most prominent and dense submarginally), subepidermal black glands also present and evident on lower surface or these lacking; young flush foliage red. *Inflorescence* a 20--35-flowered, lax, terminal raceme (rhachis not appearing as a diminuitive spinal column after flower fall); rhachis, pedicels and calyces finely puberulous, glabrescent, sometimes with red glands intermixed; bracts lanceolate, acuminate, c 3 mm long, pubescent, with or without subepidermal glands, the margins glandular, caducous; pedicels 9--10 mm long, articulated directly below to 2 mm below calyx. Calyx tube usually distinctly ribbed when dry, lobes 6--7 mm long, the lowest cucullate lobe 9 mm long, all lobes densely puberulous or pubescent on both surfaces and containing dot-dash subepidermal glands, apices fimbriate, that of lowest lobe fimbriate-glandular. *Corolla* yellow; standard petal net-veined orange, the blade oblong-elliptic to suborbicular, 11--12 x 7 mm (including a 2.5--4.5 mm claw), dorsal surface of blade densely glandular on basal $^2/_3$, the lower most glands stalked, mushroom-shaped, the uppermost sessile, dorsal surface and margin of claw densely stipitate-glandular with pin-head glands, inner surface of claw thickened and ridged, apex with two thickened ridges or sometimes with gland-tipped flanges; upper lateral petals suborbicular, 12--13 x 7--9 mm (including a 3--4 mm claw), base of blade and claw folded inwards, blade with sessile mushroom-shaped glands on basal $^1/_3$ of dorsal surface and stipitate glands on basal $^1/_3$ of margin, claw glandular on outer surface, moderately pubescent on inner surface; lower laterals subrectangular, broader near apex, 13 x 6--8 mm (including a 3 mm claw), as for upper laterals except claw less folded, less glandular and less pubescent, all 5 petals with randomly scattered, subepidermal dot glands in upper $^1/_3$--$^1/_2$ of blade or $\pm$ over whole surface of blade. Stamen filaments 10--12 mm

long, pubescent on basal $^1/_2$--$^2/_3$, some filaments of each flower stipitate-glandular on edges of upper surface; anthers 2.25 x 1 mm, sometimes stipitate glands on dorsal surface of thecae, thecal bridge thickened. Ovary pubescent, eglandular or sparsely stipitate-glandular, 5--6-ovulate; style moderately pubescent at base, becoming sparsely so towards apex, sparsely stipitate-glandular; stigma a bulbous, thickened, terminal, fringed chamber. *Fruit* a woody, explosively dehiscent, 3--6-seeded pod, 6--9.5 x 1.7--2.5 cm (including a 7--8 mm beak), margins thickened, the upper more than the lower, valves obscurely puberulous to glabrous. *Seeds* ovate-elliptic, 12 x 9 x 2 mm, brown with a tinge of olive-green, shiny. (Figs. 5S, **47** & 48C-E, Map 19).

DISTRIBUTION. Brazil in the states of Pernambuco and Bahia.

BRAZIL: Pernambuco, near Petrolina, 18 April 1971, *Heringer et al.* 63 (RB!, UB!); Serra dos Dois Irmãos, 2 Sept. 1961, *Lima* 61--3615 (RB!); Petrolina, 13 Nov. 1958, *Mors* s.n. (RB!); **Bahia**, Livramento, 26 June 1978, *de Araújo* 037 (K!); Barra, 27 June 1978, *de Assis* 219 (RB!); Villa de Barra, ?1840, *Blanchet* 3146 (holotype P, isotypes BR!, F!, GH!, K!, MG!); Mun. Livramento do Brumado, 12 March 1991, *Brito & Lewis* 293 (CEPEC!, K!); Mun. de Caculé, km 43 on road from Brumado to Caetité, 14 April 1983, *de Carvalho et al.* 1696 (CEPEC!, K!); Mun. de Brumado, c. 15 km on road from Brumado to Caetité, 27 Dec. 1989, *de Carvalho et al.* 2633 (K!); c. 23 km along road from Brumado to Livramento do Brumado, 28 Dec. 1989, *de Carvalho et al.* 2667 (K!); km 80 along road BA 052 from Irece to Xique-Xique, *Coradin et al.* 6270 (K!); near Sitio do Mato, 27 Oct. 1965, *Duarte* 9521 (K!); 64 km N of Senhor do Bonfim on BA-130 highway to Juazeiro, 25 Feb. 1974, *Harley et al.* 16308 (K!); near Aracatú, 14 May 1983, *Hatschbach* 46376 (K!); 5--15 km W of Contenda do Sincorá, 19 Sept. 1984, *Hatschbach* 48370 (K!, NY!); Rio das Rãs, Mun. Bom Jesus da Lapa, 15 Feb. 1991, *Hatschbach & Hatschbach* 55159 (K!); 15 km from Brumado on road to Livramento, 12 Dec. 1984, *Lewis et al.* CFCR 6718 (K!); 10 km S of Livramento do Brumado, 17 April 1991, *Lewis & Andrade* 1998 (BR!, CEPEC!, K!, MEXU!, NY!); 27 km S of Livramento do Brumado, 22 April 1991, *Lewis & Andrade* 2007 (BR!, CEPEC!, K!, M!, MEXU!, MO!, NY!, SI!, U!, US!); 10 km S of Livramento do Brumado, 25 March 1991, *Lewis & Andrade* 1873 (BR!, CEPEC!, K!, MEXU!, NY!); 21 km S of Livramento do Brumado, 24 April 1991, *Lewis & Andrade* 2012 (BR!, CEPEC!, K!, MEXU!, MO!, NY!, SI!); 27 km S of Livramento do Brumado, 22 April 1991, *Lewis & Andrade* 2004 (CEPEC!, K!, MEXU!, NY!); 46 km S of Livramento do Brumado, 13 March 1991, *Lewis & Andrade* 1861 (BR!, CEPEC!, K!, MEXU!, NY!); Serra do Açuruá, road from Rio Verde to Gentio do Ouro, 9 Sept. 1990, *de Lima et al.* 3924 (K!); Serra Preta, 35 km before Ipirá on BA 052 road, 7 Sept. 1990, *de Lima et al.* 3879 (K!); near Maracás, without date, *Martius* s.n. (M!); Mun. Manoel Vitorino, km 4 on road from Manoel Vitorino to Caatingal, 16 Feb. 1979, *Mattos Silva et al.* 274 (NY!).

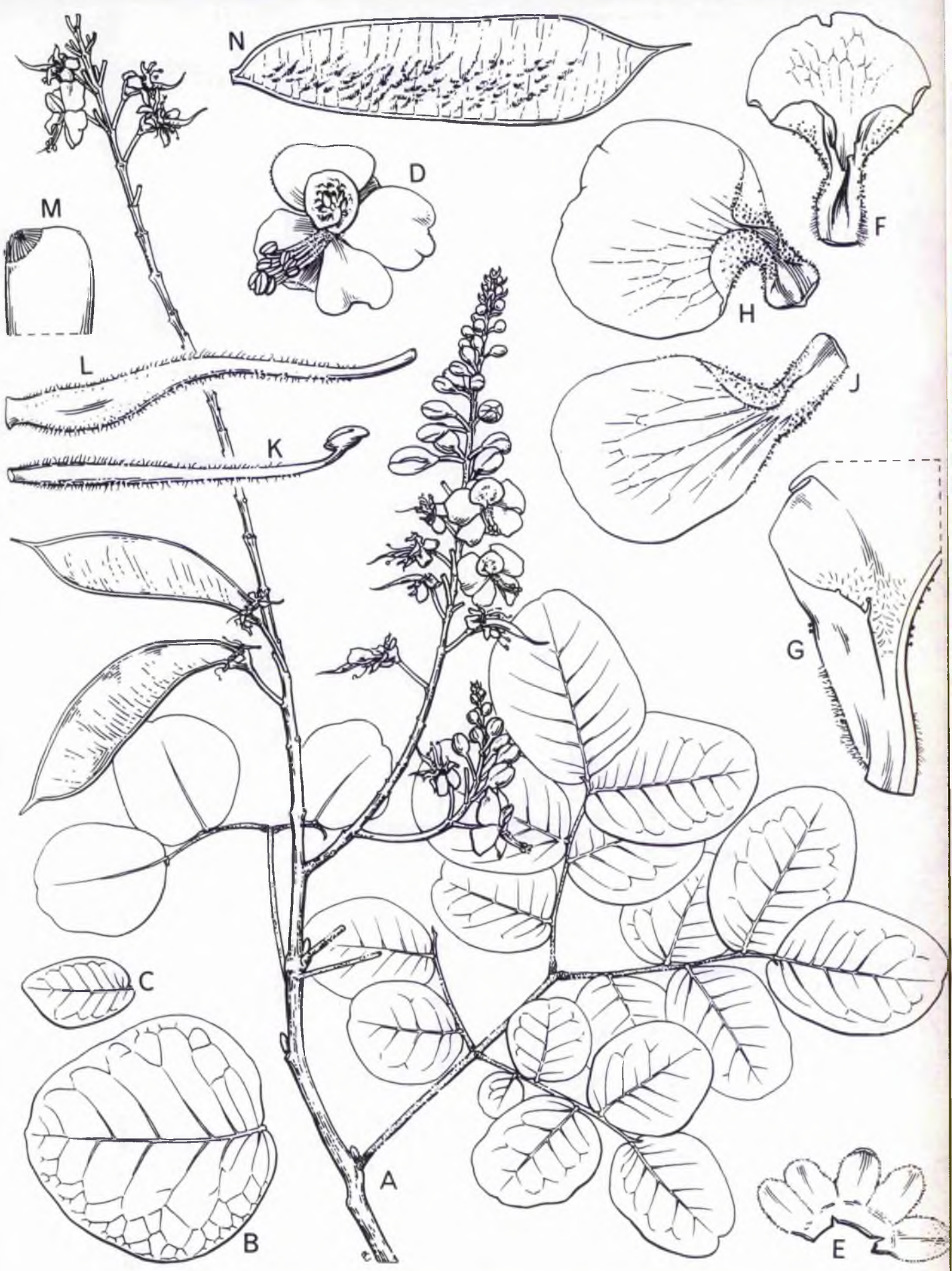


FIG. 47. *Caesalpinia laxiflora*. **A** flowering branchlet x 1; **B** leaflet undersurface x 1; **C** leaflet undersurface x 1; **D** flower x 2¼; **E** calyx opened out x 1½; **F** standard petal x 4½; **G** l.s. standard petal base x 9; **H** upper lateral petal x 4½; **J** lower lateral petal x 4½; **K** stamen x 4½; **L** gynoecium x 4½; **M** stigma x 30; **N** fruit x 1. **C** from *Lewis & Andrade* 1873, the rest from *Lewis & Andrade* 2007. Drawn by Eleanor Catherine.

FIG. 48. *Caesalpinia bracteosa*: **A** flower (*Lewis & Pearson* 1117); **B** fruit (unvouchered); *C. laxiflora*: **C** habit, Bahia, Brazil (unvouchered); **D** flowers, Bahia (unvouchered); **E** young fruits, Bahia (unvouchered); *C. microphylla*: **F** fruits, S.E. Piauí, Brazil (unvouchered).

ECOLOGY. Caatinga, c. 400---740 m.

PHENOLOGY. Flowering from February to June and from September to November, fruiting from February to June and September to December.

VERNACULAR NAMES. "Catingueira", "Catinga de porco".

NOTES. Most specimens of *C. laxiflora* are easily distinguished by a combination of lax-flowered, racemose inflorescences and broadly ovate to suborbicular,wavy-margined leaflets. A few specimens show characters that intergrade with those of other, closely related species, and, occasionally, natural hybrids can be supposed although, to date, no experimental work has been carried out that substantiates this. *Harley et al.* 16308A from 64 km north of Senhor do Bonfim in Bahia might represent a hybrid between *C. laxiflora* and *C. microphylla*. *Ramalho* 22 from Petrolina in Pernambuco may also be the result of a cross between the same two parents. It appears to be a small-leafleted *C. laxiflora* with a larger than usual number of pinnae (4 pairs plus a terminal) and leaflets (up to 15 per pinna). *Mori et al.* 11246 from highly disturbed caatinga along the road between Manoel Vitorino and Caatingal might be a natural hybrid between *C. laxiflora* and *C. pluviosa* var. *peltophoroides*. Its leaflets are smaller than is usual for *C. laxiflora* and larger than those of *C. pluviosa* var. *peltophoroides*. The stems bear plumose, stipitate glands, the petal dorsal surfaces are glandular and the petal and sepal blades have subepidermal idioblasts in them.

32. **Caesalpinia microphylla** *Mart. ex G. Don*, Gen. Syst. 2: 431 (1832). Type: Brazil, Bahia, in sylvis catingas, *Martius* Obsv. 2274 (lectotype M!, chosen here, isolectotypes K!, M!).

Unarmed multiple-stemmed, viscid shrub to small tree, 0.5--5 m tall; bark rough, pale grey, brown or mottled grey and black; stems sparsely puberulous, glabrescent or moderately pubescent with ± curved hairs, stipitate glands intermixed with the pubescence. *Leaves* bipinnate; stipules early caducous; petiole 1--1.5 cm long, pubescent, stipitate-glandular, often densely so; rhachis 3--9 cm long, densely spreading pubescent and stipitate-glandular; pinnae in 3--10 alternate to opposite pairs plus a terminal pinna; leaflets subsessile with a short petiolule, alternate to subopposite, 11--21(--22) per pinna,

oblong-elliptic to suborbicular, apex rounded, 1.5--10(--12) x 1--7(--10) mm, margin revolute and usually long-ciliate, blade surfaces sparsely to moderately pubescent, glabrescent; venation obscure, main vein excentric, secondary venation brochidodromous; short-stalked glands sparse to moderately dense on lower surface, usually randomly scattered, sometimes reduced to a single gland in each loop of the secondary venation, often appearing as shiny, pale yellow, globular secretions; stalked glands clustered at base of petiolules, additionally some dark, subepidermal glands in the leaflet margins. *Inflorescence* a terminal or lateral raceme, rhachis, pedicels and calyces finely puberulous to densely pubescent, densely stipitate-glandular, the gland stalks often hairy; bracts lanceolate-acuminate, 2--3 mm long, pubescent, stipitate-glandular, caducous; pedicels 8--13 mm long, articulated 2--2.5 mm below calyx. *Calyx* lobes 5--6.5 mm long, inner surfaces densely tomentose, lower lobe cucullate, distinctly larger than other 4, c. 8 mm long, apex densely glandular-fimbriate. *Corolla* yellow; standard petal with orangish-red markings, blade subquadrate, 10 x 5--6 mm (including a 3--4 mm claw), dorsal surface of blade sparsely stipitate-glandular with small glands, claw thickened with two longitudinal ridges but lacking apical appendages, dorsal surface glandular; upper lateral petals broadly obovate to suborbicular, 13 x 10--11 mm (including a 2--2.5 mm claw), dorsal surface of blade and claw stipitate-glandular, claw twisted, folded inwards, margin densely stipitate-glandular and pubescent, inner surface sparsely to moderately pubescent; lower laterals obovate, 12--13 x 8--9 mm (including a 2 mm claw), dorsal surface of blade and claw stipitate-glandular, claw twisted, less glandular and pubescent than upper laterals, one to a few subepidermal glands in upper $^1/_2$ of blade. Stamen filaments 9--12 mm long, pubescent on basal $^1/_2$--$^2/_3$ (especially basal $^1/_2$), individual flowers have some filaments eglandular, others moderately glandular with short-stalked, pixie-cup glands on the middle portion (not at base or apex); anthers 1.5 x 0.75 mm, with a prominent, thickened, apical thecal bridge. Ovary spreading pubescent with long hairs, especially along the margins, densely glandular with sessile and stalked glands; style curved, c. 8 mm long, stipitate-glandular and spreading pubescent on the basal $^2/_3$; stigma a terminal, thickened, fringed chamber. *Fruit* a woody, explosively dehiscent pod, 6.6--9 x 1.5--1.85(--2.2) cm (including a beak of up to 7 mm), upper margin thickened, c. 3 mm wide, valves sparsely to moderately pubescent, glabrescent, hairs most evident on the suture, densely glandular,

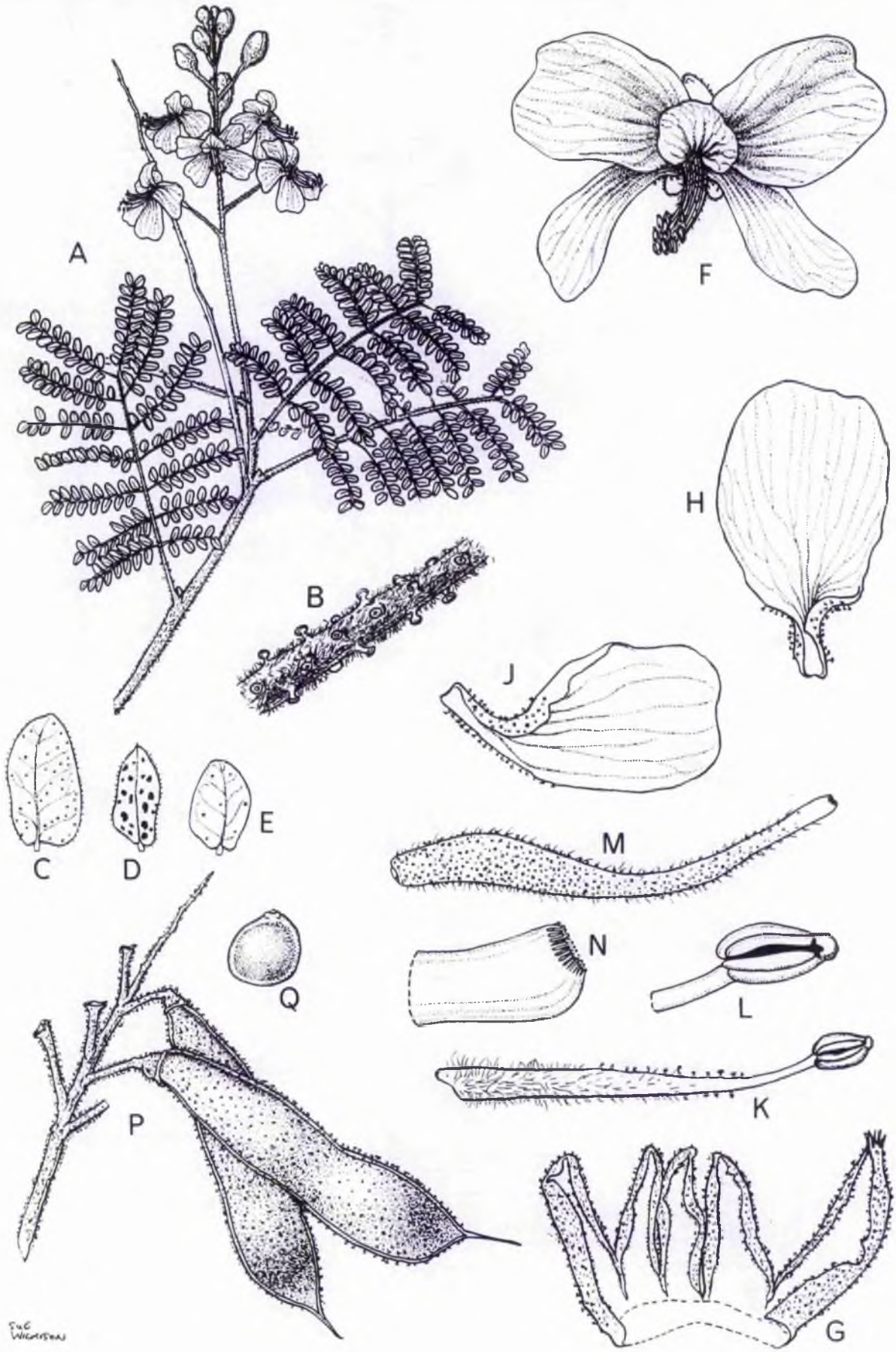
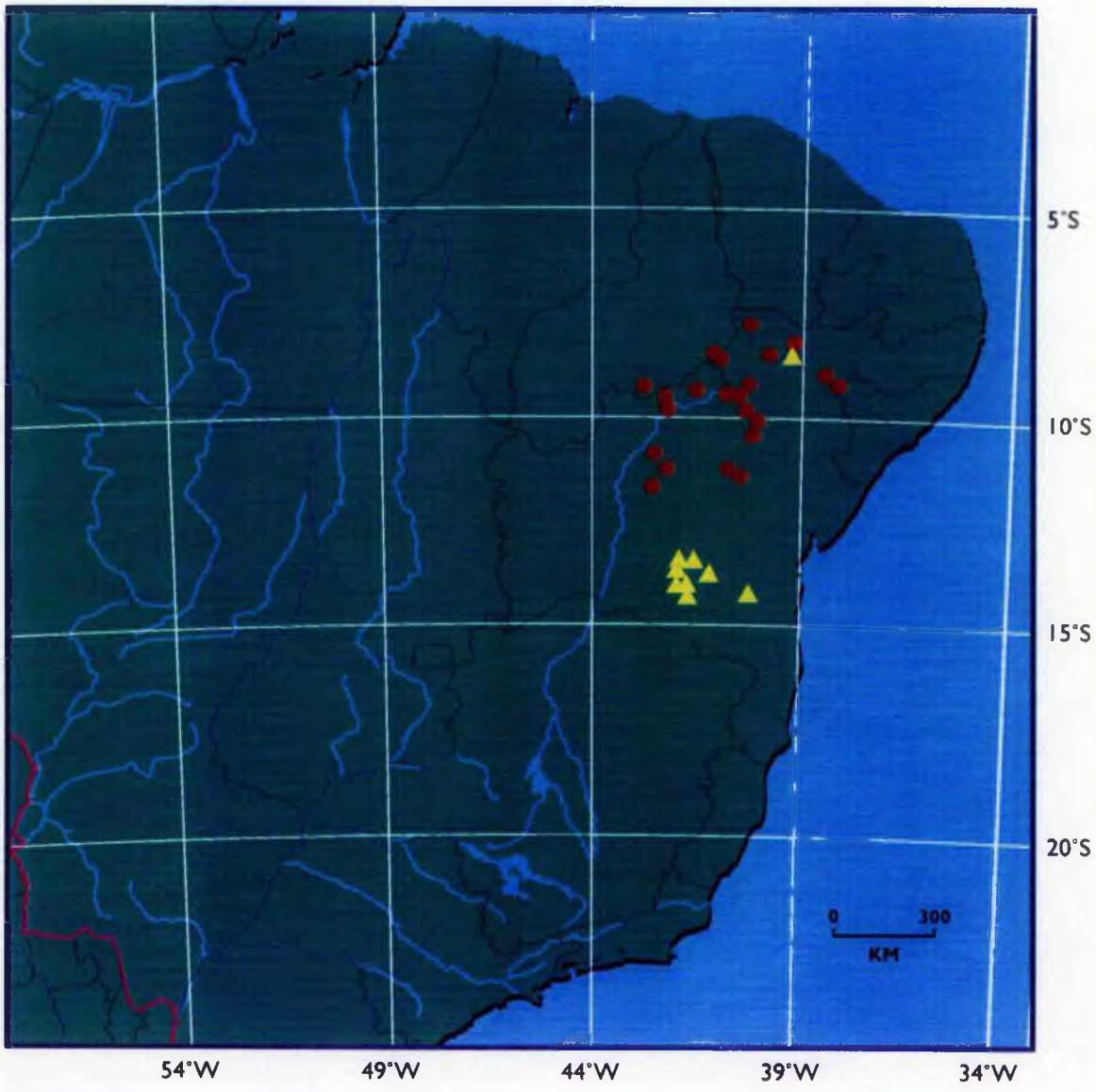


FIG. 49. *Caesalpinia microphylla*. **A** inflorescence & foliage x 1; **B** glandular leaf rhachis x 12; **C** median leaflet undersurface x 3; **D** & **E** median leaflets undersurfaces (to show range) x 6; **F** flower x 4½; **G** calyx opened out x 6; **H** standard petal x 6; **J** upper lateral petal x 6; **K** stamen x 9; **L** anther x 18; **M** gynoecium x 9; **N** stigma x 30; **P** fruits x 1; **Q** seed x 1½. **A** & **E–N** from *Lewis & Pearson* 1072, **D** from *Eiten & Eiten* 10872, **B**, **C**, **P** & **Q** from *Coradin et al.* 5941. Drawn by Sue Wickison.

Distribution of *Caesalpinia calycina* (△) and *C. microphylla* (●) in Brazil



2--4(--6)-seeded. *Seeds* broadly ovate, 9--10 x 8--9 x 1.5--2 mm, olive green-brown, shiny. (Figs. 9E, 48F & **49**, Map 17).

DISTRIBUTION. Brazil in the states of Piauí, Pernambuco and Bahia.

BRAZIL: Piauí, without exact locality, without date, *Luetzelburg* 385 (F!, M!); Fundação Ruralista, 24 Nov. 1981, *Pearson* 37 (K!); 1 Dec. 1981, *Pearson* 58 (K!); **Pernambuco**, Petrolina, near the Rio São Francisco, 22 Jan. 1970, *Carauta* 999 (RB!); Petrolina, Lagoinha, Propriedade dos Borges, BR-428, km 188, 11 March 1982, *Cavalcanti et al.* CFPE 214 (F!); near Petrolina, 12 May 1918, *Curran* 239 (F!), 239a (GH!, NY!); without exact locality, 12 Sept. 1954, *Falcão* 1046 (NY!, UB!); without exact locality, 26 Nov. 1978, *Leitão Filho & Timoni* 8902 (E!, MBM!, MG!, UEC!); between Serra Talhada and Petrolina, 17 April 1971, *Heringer et al.* 57 (UB!); Santa Maria da Boa Vista, 29 April 1971, *Heringer et al.* 390 (RB!, UB!); Ouricuri, near Barra de S. Pedro, 2--9 Jan. 1961, *Lima* 61--3604 (RB!); Serra dos Dois Irmãos, 2--9 Jan. 1961, *Lima* 61--3614 (RB!); Petrolandia, 8 May 1950, *Lima* 50--541 (RB!); Cachoeira do Roberto, 1913, *Luetzelburg* 5 (M!); Terra Nova, 1912, *Luetzelburg* 1283 (5937) (RB!); Petrolandia, 15 Aug. 1948, *Monteiro Neto* 3 (RB!); Petrolina, aeroporto, 7 Sept. 1981, *Orlandi* 525 (K!, UB!); **Bahia**, Serra de Jacobina, ?1835, *Blanchet* 2684 (BR!, F!, K!); Tamanduá, June 1844, *Blanchet* 3825 (BR!, F!); between Barrinha and Itamirim,18 Dec. 1922, *Compos Porto* s.n. (RB No. 19092) (RB!); Serra do Açuruá, road Rio Verde to Gentio do Ouro, 4--5 km past Tiririca, 9 Sept. 1990, *Cavalcante de Lima* et al. 3927 (K!); without exact locality, 1840, *Claussen* s.n. (F!); Mun. Nov. Remanso, road Novo Remanso to Petrolina, km 74, 22 June 1983, *Coradin et al.* 5941 (K!); 11 km S of Juazeiro, without date, *Eiten & Eiten* 10872 (K!, NY!); Mun. de Jacobina, near Lajes, 2 Sept. 1981, *Ferreira* 77 (K!, UB!); Serra do Açuruá, between São Inácio and Xique-Xique, c 24 km N of São Inácio, 28 Feb. 1977, *Harley et al.* 19163 (K!); 64 km N of Senhor do Bonfim on BA-130 road to Juazeiro, 25 Feb. 1974, *Harley et al.* 16301 (K!); c 40 km along the BR-235 road from Petrolina to Casa Nova, 15 Jan. 1982, *Lewis & Pearson* 1072 (K!); Tanque Novo, without date, *Luetzelburg* 711 (M!); without exact locality, without date, *Martius* s.n. (mss. 2274) (K!, M!); Remanso, BR-235, 20 Nov. 1979, *Miranda* 294 (F!); Mun. Central, 11°11'S, 42°07'W, 31 March 1984, *Salgado & Bautista* 331 (RB!); Mun. Jaguarari, 64 km E of Juazeiro towards Senhor do Bonfim, 8 Jan. 1991, *Taylor et al.* 1373 (BR!, K!, M!, MEXU!, NY!, US!, Z!); Mun. Juazeiro, 7 km S of Juazeiro, 24 Jan. 1993, *Thomas et al.* 9617 (K!); near Remanso, Jan. 1907, *Ule* 7196 (F!, HBG!, K!).

ECOLOGY. Caatinga on sandy soil, 340-- c 600 m.

PHENOLOGY. Flowering and fruiting from November to June and occasionally into September.

VERNACULAR NAMES. "Catinga de porco" (Bahia), "Catingueira rasteira" (Bahia and Pernambuco).

NOTES. The foliage is reported to be a useful forage and a medicinal tea to cure colds and stomach upsets is made from an infusion of the leaves. *Taylor* (number 1373) describes the plant as being slightly aromatic.

The species is one of a small number of north east Brazilian *Caesalpinia* species forming dominant stands in the caatinga vegetation. Essentially the species differs from all closely related ones by a combination of small glandular leaflets, few-flowered racemes with densely glandular rhachides and pedicels and generally smaller fruits. Nevertheless, a small number of specimens seem to be intermediate between *C. microphylla* and closely related taxa and in two cases might represent natural hybrids. *Carauta* 998, from Pernambuco, appears intermediate between *C. microphylla* and *C. laxiflora* and might be of hybrid origin and *Queiroz* 551 from the ecological station of Rasa da Catarina in Bahia is atypical and might also be of hybrid origin. The latter bears the vernacular name "Catingueira pem-pem", unrecorded for any other Brazilian *Caesalpinia* and further indicating the plants distinctness.

33. **Caesalpinia pluviosa** DC., Prodr. 2: 483 (1825).

Type: Brazil, *Leandro di Sacramento*? 7819 (holotype P, n.v.).

Unarmed shrub to medium-sized tree, sometimes multiple-stemmed from the base, (2--)5--20(--25) m tall, DBH (3--)20--40(--80) cm, trunks of some older specimens quadrate-fluted; bark grey or brownish grey, smooth or rugose and rough, scaling off in vertical elongated flakes or thick rectangular chunks; branchlets with whitish grey, ovate, prominent lenticels, young branchlets densely tomentose, glabrescent or glabrous. *Leaves* bipinnate; petiole 1--3.5(--4) cm long, pubescent, sometimes with a few red glands intermixed, or glabrous; rhachis (1.5--)3.5--13.5(--15) cm long, densely pubescent, usually with red, stipitate glands intermixed with the indumentum or glabrous; pinnae in 2--11 opposite to alternate pairs plus a terminal pinna (or occasionally ending in a pair); leaflets 9--29(--31) per pinna, alternate (the terminal pair sometimes opposite), sessile, coriaceous, terminal leaflets obovate to ± oblong-rhombic, apex rounded, base cuneate to truncate, (5--)6--33 x 2.5--18 mm, median leaflets oblong-elliptic, rectangular or subrhombic, (4.5--)5--29(--38) x (2.5--)3--15(--18) mm, apex rounded to acute, base

inequilaterally truncate, the margin sometimes revolute, all leaflets sparsely spreading pubescent to glabrous (but for a ciliate margin) or glabrous and nitid on upper surface, sparsely to moderately pubescent on lower surface, at least on the main vein and sometimes the secondary veins also; the main vein excentric, oblique, prominent on the lower surface, secondary veins brochidodromous; reddish black epidermal or subepidermal glands scattered over the surface of the leaflet blades, these most evident on the young foliage of saplings and seedlings, most obscure on mature leaflets where they are best seen near the midvein or along the leaflet margin, midvein apex usually terminating in a dark gland. *Inflorescence* a terminal, often showy panicle of 4--18 aggregated racemes, each raceme with 25-- c 100 flowers, less often an axillary or terminal, densely-flowered raceme of up to 140 flowers, the rhachides of very young inflorescences often with densely stellate or plumose hairs, mature inflorescences with the rhachis, pedicels and calyces moderately tomentulose to densely rusty brown tomentose; bracts ovate-lanceolate, acuminate, (1.5--)2.5--6 mm long, tomentulose, a few subepidermal glands in blades, caducous; pedicels (4--)8--20 mm long, held erect, articulated directly below to 1.5(--2.5) mm below calyx. *Calyx* lower lobe cucullate, 7--9 mm long, the margin glandular-fimbriate, the other 4 lobes (4.5--)5--7 mm long, slightly fimbriate or ragged at apices, sometimes with subepidermal glands in blades. *Corolla* yellow, the standard petal spotted or net-veined orange, blade suborbicular, broadly ovate, to depressed elliptic or spathulate (when thickened claw included), c(6--)8--12 x (4--)7--8 mm (including a 2--3 mm claw), dorsal surface of claw and blade stipitate-glandular, sometimes densely so over whole surface of blade, claw pubescent on the margins of its base, inner surface ribbed, pubescent, the apex slightly flanged and glandular or with two distinct, fleshy fimbriate ridges, the fimbriae gland-tipped, occasionally two secondary ridges within the first pair; upper lateral petals with blade suborbicular to broadly ovate, 10--14 x 7--12 mm (including a 2--3 mm claw twisted to one side), base of blade and claw margin folded, stipitate-glandular, the inner surface of claw pubescent; lower laterals with blade obovate to elliptic-rectangular, 11--14 x 5.5--10 mm (including a (1--)2--2.5 mm claw), claw and blade base not folded, inner surface of claw sparsely pubescent, margin stipitate-glandular, all four laterals sparsely to moderately dotted with subepidermal glands, dorsal surfaces of blades eglandular or with glands restricted to intervenal furrows. Stamen filaments 11--17 mm long, pubescent on basal $^1/_3$--$^2/_3$ (densely so on basal $^1/_3$), stipitate-glandular at least on

basal $^{2}/_{3}$, sometimes along entire length; anthers 1.5--1.75 x 0.75--1 mm, usually with a dark gland in the thecal bridge. Ovary moderately to densely pubescent, usually with short curled hairs and long straight hairs intermixed, glandular with sessile or short-stalked glands, c 5--6-ovulate; style (7--)9--14 mm long, pubescent and stipitate-glandular along its entire length, slightly thickened towards apex; stigma a terminal or subterminal, fringed chamber. *Fruit* an explosively dehiscent woody pod, 8--13.5(--16) x 2--3.3(--3.7) cm (including a 3--15 mm long apical beak), the upper margin thickened or ridged on each side, 3--7 mm wide, at maturity the valves glabrous and eglandular or with a few scattered hairs and reddish glands, strongly reticulate-veined, (3--)4--6-seeded. *Seeds* ochre or buff coloured, 15--19 x 10--12 x 1 mm.

33a. var. **pluviosa**

Caesalpinia floribunda Tul. in Archiv. Mus. Hist. Nat. Paris 4: 140 (1844). Type: Bolivia, Prov. de Chiquitos, camino de San Rafael a Santa Ana, without date, *Orbigny* 1039 (holotype P!, isotype G).

Caesalpinia taubertiana S. Moore in Trans. Linn. Soc. London, Bot. 4: 345 (1895). Type: Brazil, near Corumbá, Jan. 1891--1892, *Moore* 1037 (holotype BM!, isotype BM!).

Leaf rhachis 3.5--13.5 cm long, pinnae in 3--11 pairs plus a terminal pinna (or this lacking), leaflets 18--29 per pinna, terminal leaflets 6--22 x 2.5--12 mm, inflorescence a panicle, stamen filaments 11--13 mm long. (Fig. **50**, Map 22).

DISTRIBUTION. Western Brazil, Bolivia, Paraguay and northern Argentina.

BRAZIL: Mato Grosso, road Caceres to S of Serra do Aguapei, km 134, 4 March 1977, *Kirkbridge & Lleras* 3074 (BR!, F!, INPA!, K!, NY!, US!); Rio Paraguai, fazenda Acurizal, 57°32'W, 17°52'S, June 1979, *Prance & Schaller* 26690 (NY!); same locality and date, *Prance & Schaller* 26693 (NY!); Vila Maria [= Caceres], without date, *Riedel* s.n. (A!); near Vila Maria, without date, *Riedel* 520 (K!); fazenda Bela Vista, Rio Paraguai, 15 March 1976, *Schaller* 84 (NY!); road from Miranda to Campão, 15 Dec. 1976, *Shepherd et al.* 4125 (MBM!, NY!, UEC!); **Mato Grosso do Sul,** Corumbá, 25 July 1982, *de Paula & Conceição* 1539 (US!); Corumbá, Jan. 1940, Miranda, 28 Jan. 1979, *Mattos Filho* 1050 & *Neto* (RB!); *Froes* 11691 (F!, K!, NY!); Corumbá, 2 Dec. 1920, *Malme* 2710 (A!, F!); Corumbá, 3 April 1930, *Malme*

2710a (F!); Corumbá, 22 Nov. 1987, *Ratter & Pott* R6078 (E!, K!); Corumbá, 22 Nov. 1987, *Ratter & Pott* R6076 (E!, K!); Corumbá, 9 Oct. 1985, *Ratter et al.* R5140V (E!, K!); Corumbá, 20 Dec. 1902, *Robert* 740 (K!); Porto Murtinho, 18 March 1985, *Hatschbach & Zelma* 49291 (K!, NY!); Serra do Urucum, 15 April 1972, *Hatschbach* 29508 (K!, MBM!, NY!); Mun. Porto Murtinho, Morro do Chapéu, 18 March 1985, *Hatschbach & Silva* 49255 (K!); 60 km W of Miranda, 28 Jan. 1979, *Krapovickas & Cristobal* 34437 (NY!); **BOLIVIA.** Depto. Beni, Prov. Ballivián, Misión Fatima, 28 May 1988, *Beck et al.* 16628 (NY!); Depto Tarija, Prov. Arce, Bermejo, 22 Dec. 1979, *Coro-Rojas* 1439 (NY!); near Jacuiba, Nov. 1910, *Herzog* 1063 (M!); Depto. Santa Cruz, Prov. Cordillera, 5 km N of Yatarenda, 63°32'W, 19°12'S, 17 April 1977, *Krapovickas & Schinini* 31490 (NY!); Alto Parapeti, 8 Jan. 1982, *Michel* 155 (NY!); same locality, 16 Jan 1980, *Michel* 56 (NY!, US!); Prov. Andres Ibanez, 12 km E of Santa Cruz, 18 Feb. 1988, *Nee* 36347 (K! TEX!); same locality, 5 Dec. 1988, *Nee* 37023 (K!, TEX!); 2 km NW of Puerto Pailas, 17 Dec. 1991, *Nee* 42136 (K!); 3 km SE of Cotoca, 17 Nov. 1990, *Nee* 40000 (K!); Prov. Ichilo, 2 km SW of Buena Vista on road to El Cairo, 8 Dec. 1990, *Nee* 40266 (K!, TEX!); Prov. Andres Ibanez, 3 km NW of Cotoca, 21 Dec. 1989, *Nee* 38223 (K!, TEX!); Prov. Florida, road Bermejo to Santa Cruz, 14 Dec. 1991, *Nee* 42103 (K!); 12 km SE of Comunidad Don Lorenzo, 17 Nov. 1990, *Nee & Coimbra* 39998 (K!); Prov. Nuflo de Chavez, 1 km E of San Javier, 30 Nov. 1990, *Nee & Coimbra* 40095 (K!); c 12 km NW of San Javier, 30 Nov. 1990, *Nee & Coimbra* 40112 (K!); 64 km S of Santa Cruz, 24 Nov. 1990, *Pennington et al.* 13321 (CR!, K!, NY!, U!); Santa Cruz, 15 Dec. 1988, *Roca* 202 (K!); Prov. Velasco, San Ignacio, 26 April 1986, *Seidel & Beck* 188 (K!, NY!); Borgues de Buenavista, 21 Nov. 1924, *Steinbach* 6702 (A!, F!, K!, NY!); Santa Cruz, 1 Dec. 1987, *Thomas* 5559 (K!,NY!); Choreti, 10 Nov. 1927, *Troll* 183 (M!); Nuflo de Chavez, 90 km SE of Concepcion, 25 July 1985, *Killeen* 1078 (TEX!); Depto. Chuqisaca, Prov. H. Siles, Piraimiri, 17 Nov. 1988, *Murguía & Muñoz* 190 (K!); Prov. of Chiquitos, without complete date, *Orbigny* 1039 (BR!, F!, P!); Prov. Cordillera, 23 Jan. 1945, *Peredo* 49 (NY!); west Valasco, July 1892, *Kuntze* s.n. (NY!); **PARAGUAY.** Cerro Morriño, 50--60 km N of Fuerte Olimpo, 29 March 1980, *Bernardi* 20398 (NY!); between Rio Apa and Rio Aquidaban, Dec. 1908/09, *Fiebrig* 4519 (E!, K!); same locality, 11 Dec. 1908/09, *Fiebrig* 4396 (E!, GH!, K!, M!); **ARGENTINA.** Prov. Salta, Depto. Gran, near Dique Itiyuri, 17 March 1972, *Legname & Cuazzo* 9044C (GH!); Salta, Tartagal, 15 Oct. 1945, *Di Lella & García* 2807 (K!); Depto. Orán, Tartagal, 7 Dec. 1941, *Maldonado* 822 (F!); Depto. San Martín, Pocitos, 20 Feb. 1954, *Meyer* 18313 (GH!); Tartagal to Tanja Honda, 6 Feb. 1940, *Schreiter* 11097 (F!); Depto. Orán, Piquirenda, 16 Feb. 1925, *Schreiter* 3837 (A!); Tartagal, 5 July 1944, *Schulz & Varela* 5096 (NY!).

ECOLOGY. Cerradão; remnants of deciduous forest; secondary vegetation on calcareous soil; dry sandy soils of the pantanal, c 400--800 m.

PHENOLOGY. Flowering and fruiting from November to April with fruits sometimes persisting until October.

VERNACULAR NAMES. "Faveira", "Sicupira", "Coração de negro" (Brazil); "Chari", "Momoquí" (Bolivia).

FIG. 50. *Caesalpinia pluviosa* var. *pluviosa*. **A** flowering branch x 1; **B** median leaflet undersurface x 3; **C** stellate indumentum on inflorescence rhachis x 60; **D** bract x 12; **E** flower front view x 3; **F** flower side view x 3; **G** calyx opened out x 3; **H** standard petal x 4½; **J** l.s. standard petal x 7½; **K** upper lateral petal x 4½; **L** lower lateral petal x 4½; **M** stamen x 6; **N** gynoecium x 6; **P** stigma x 12; **Q** fruit x 1. **A** & **C** from Roca 202, **B** & **Q** from *Seidel & Beck* 188, **D**–**P** from *Pennington et al.* 13321. Drawn by Eleanor Catherine.

NOTES. *Caesalpinia pluviosa* var. *pluviosa* is the correct name for the plant more commonly known as *C. floribunda*. A detailed survey of *C. pluviosa*, two closely related species (*C. paraensis* and *C. peltophoroides*) and three new taxa has resulted in these being recognised here as infraspecific taxa within the *C. pluviosa* 'complex'. These varieties display a degree of character overlap between each other but distinct entities can be recognised and associated with different geographical distributions. Ulibarri (1991) placed both *C. paraensis* and *C. peltophoroides* in synonomy under *C. pluviosa* but, while this decision is undoubtedly pragmatic from a plant identification standpoint, it obscures a fascinating character evolution in *C. pluviosa* that can be related to geography. In the present treatment, six varieties are proposed in *C. pluviosa* but some reshuffling might prove necessary after additional fieldwork.

Ratter and Pott (R6078) record that the fruits of *C. pluviosa* explosively dehisce with such force that the seeds can be ejected up to 20 metres.

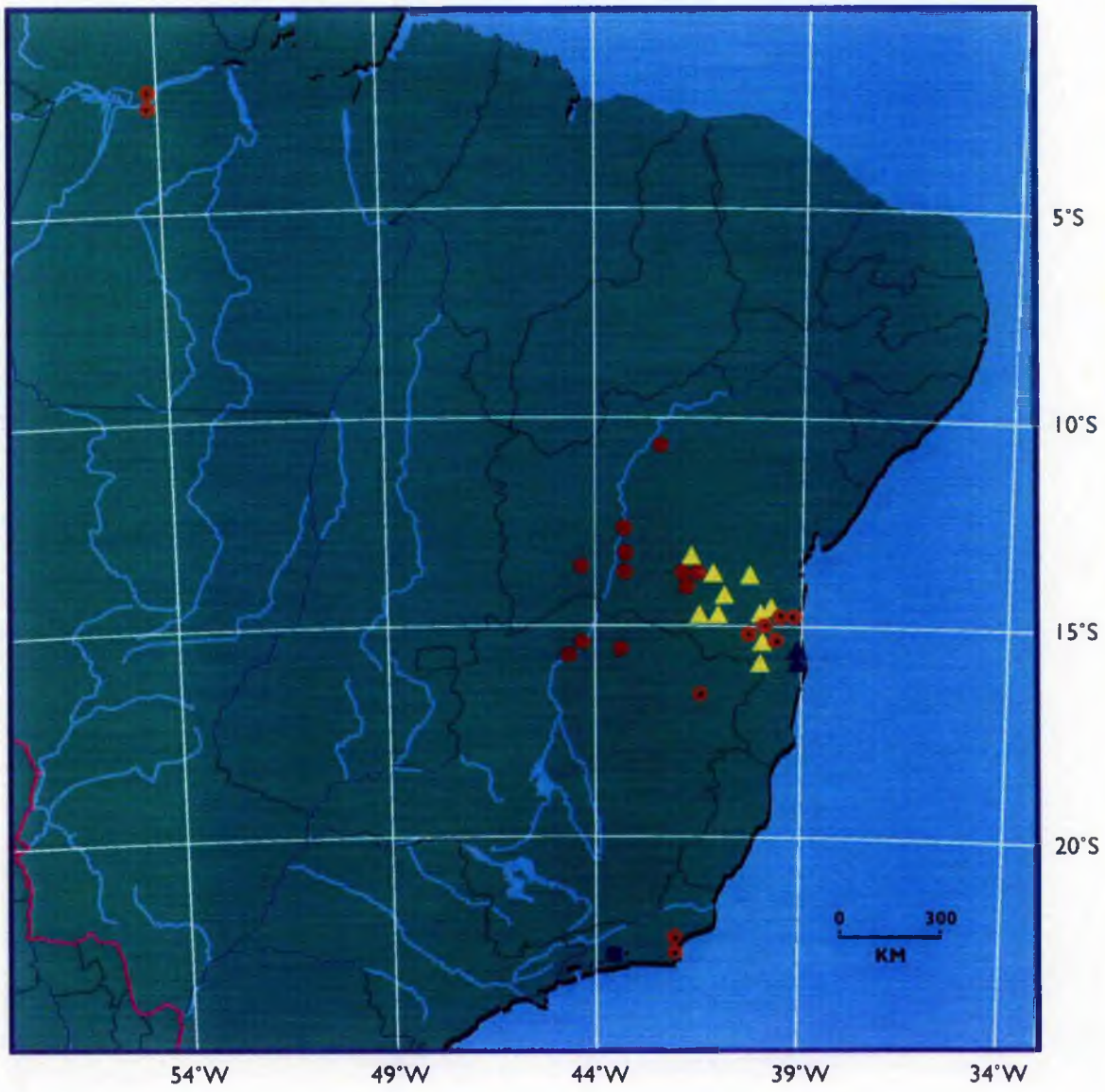
33b. var. **intermedia** *G.P. Lewis*, var. nov., in sched. Type: Brazil, Bahia, Abaíra, road to Jussiape, 15 Feb. 1987, *Harley et al.* 24326 (holotype SPF, isotype K!).

Leaf rhachis 6--7 cm long, pinnae in 4--6 pairs plus a terminal pinna, leaflets 13--20 per pinna, terminal leaflets 6--8 x 4--4.5 mm, inflorescence a raceme, stamen filaments 7--10 mm long. (Map 18).

DISTRIBUTION. Brazil, restricted to south eastern Bahia and north eastern Minas Gerais.

BRAZIL: Bahia, Contendas do Sincorá, 24 Oct. 1978, *Araújo* 104 (RB!); Mun. de Tremedal, road Tremedal to Venda Velha, 14 March 1984, *Brazão* 273 (CEPEC!, RB!); Mun. de Poções, road to Caldeirão, 16 March 1984, *Brazão* 276 (CEPEC!, RB!); Abaíra, road to Jussiape, 15 Feb 1987, *Harley et al.* 24326 (isotype K!); Mun. de Vitória da Conquista; fazenda Chapada Velha, 31 March 1984, *Lima & de Oliveira Filho* 94 (CEPEC!); Jequié, without date, *Pinheiro* 96 (CEPEC!, UB!); Almadina, road to Ibitupan, 12 March 1971, *Pinheiro* 1136 (CEPEC!, US!); Itajú do Colônia, 12 km along road to Feirinha, 23 Oct. 1969, *dos Santos* 442 (CEPEC!); **Minas Gerais**, 8 km west of Salto da Divisa, 19 Nov. 1989, *Hatschbach & Cordeiro* 52726 (K!).

Distribution of *Caesalpinia pluviosa* var. *cabraliana* (▲) var. *intermedia* (△) var. *paraensis* (●) var. *peltophoroides* (■) (excluding cultivated collections) and var. *sanfranciscana* (●) in Brazil



ECOLOGY. Caatinga and mata galeria, up to 600 m.

PHENOLOGY. Flowering October to March, fruiting February and March.

VERNACULAR NAMES. "Quebra façăo", "caatingueira de folha miúda".

NOTES. This variety is intermediate between the next two, namely var. *peltophoroides* and var. *cabraliana*. The stature of the plant and the size of the flowers are generally smaller in var. *intermedia* than in the other two. Young stems usually have a dense covering of plumose or dendritic trichomes which are sometimes gland-tipped or have relatively long, dark red terminal branches, contrasting with the translucent basal appendages of the trichome. These elaborate trichomes are commonly clustered in the leaflet insertions. The pedicels occasionally have a few sessile, globose glandular structures on them but these are not common. The outer face of the standard petal blade is moderately glandular with sessile, ± globose glands on the basal $^{2}/_{3}$--$^{3}/_{4}$. Similar, sessile or short-stalked glands also occur on the dorsal surfaces of the four lateral petals near the base. *Pinheiro* 1123 seems intermediate between var. *intermedia* and var. *peltophoroides*. It was collected from a 25 metre tree growing in a cocoa plantation and has larger leaves than typical var. *intermedia*. The leaf rhachis attains 13.5 cm, the petiole 2.9 cm, each leaf has up to 12 pairs of pinnae and each pinna up to 28 leaflets. The fruit measures up to 13 x 3.7 cm and the upper margin of the suture is ridged. All these characters fall within the range seen in var. *peltophoroides*.

33c. var. **peltophoroides** (*Benth.*) *G.P. Lewis* stat. & comb. nov., in sched.

Caesalpinia peltophoroides Benth. in Mart. Fl. Bras. 15(2): 72 (1870). Syntypes: Brazil, Rio de Janeiro, *Glaziou* 1032 (BM!, BR!, F!); *Glaziou* 6 (BR!).

Leaf rhachis 5--14(--15) cm long, pinnae in 6--11 pairs plus a terminal pinna, leaflets 19--31 per pinna, terminal leaflets 5--11 x 3--5.5 mm, inflorescence a raceme, stamen filaments 10--22 mm long. (Fig. **51** & 52A-D, Map 18).

DISTRIBUTION. Apparently indigenous to eastern Brazil, also widely cultivated in many Brazilian cities as an ornamental street tree, cultivated in Bolivia and Colombia.

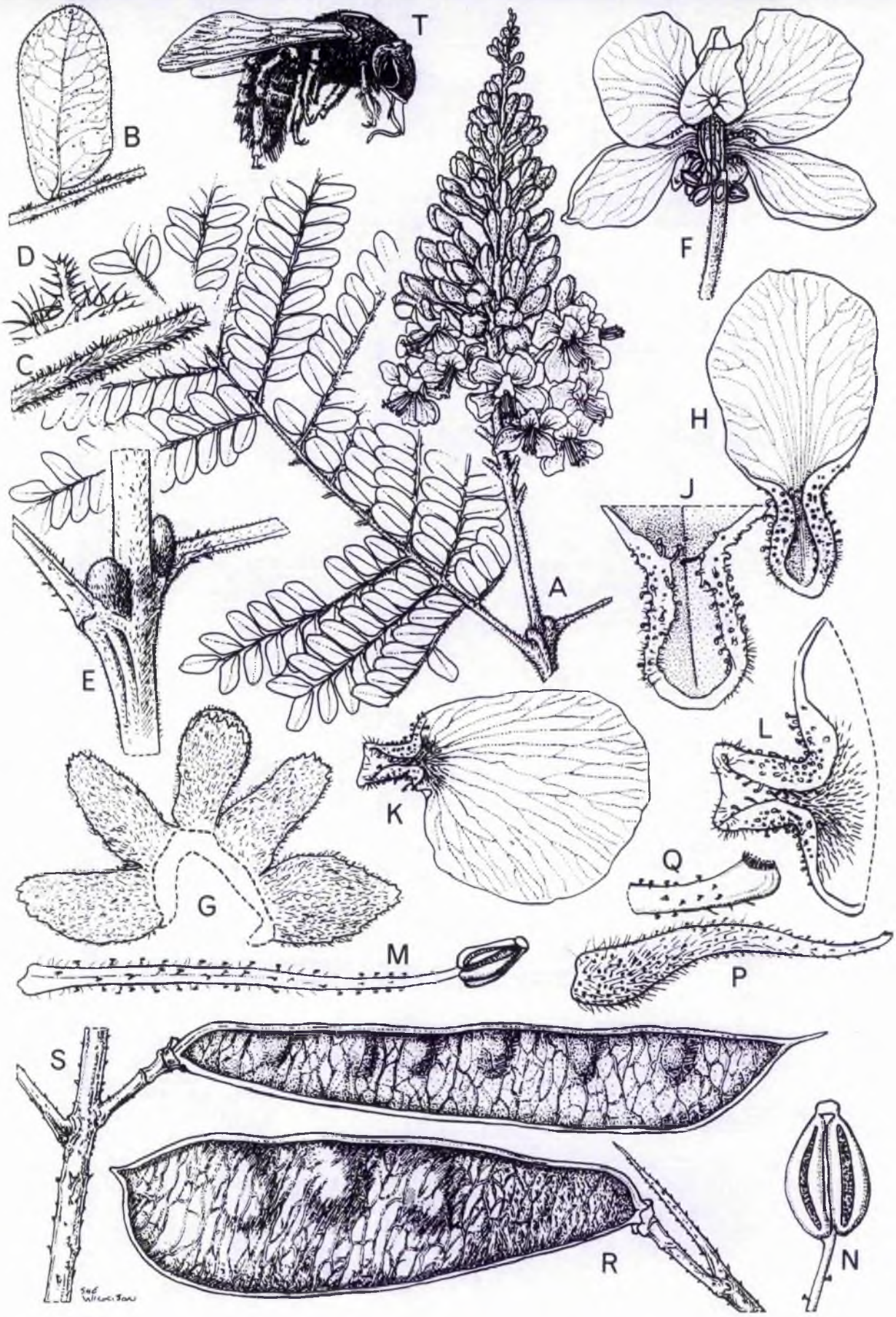


FIG. 51. *Caesalpinia pluviosa* var. *peltophoroides*. **A** inflorescence and foliage x 1; **B** leaflet undersurface x 4½; **C** leaf rhachis detail x 9; **D** detail of plumose glands on leaf rhachis x 40; **E** buds in axes of leaf petioles x 3; **F** flower x 3; **G** calyx opened out x 6; **H** standard petal x 6; **J** detail of standard petal claw x 9; **K** lateral petal x 6; **L** lateral petal claw x 9; **M** stamen x 9; **N** anther x 18; **P** gynoecium x 9; **Q** stigma x 15; **R** & **S** fruits x 1; **T** pollinator – *Xylocopa* sp. x 1½. **A–Q** from *Lewis* 1604, **R** from *Lewis* s.n., **S** from *Silverstone-Sopkin* 5953, **T** collected on *Lewis* 1604. Drawn by Sue Wickison.

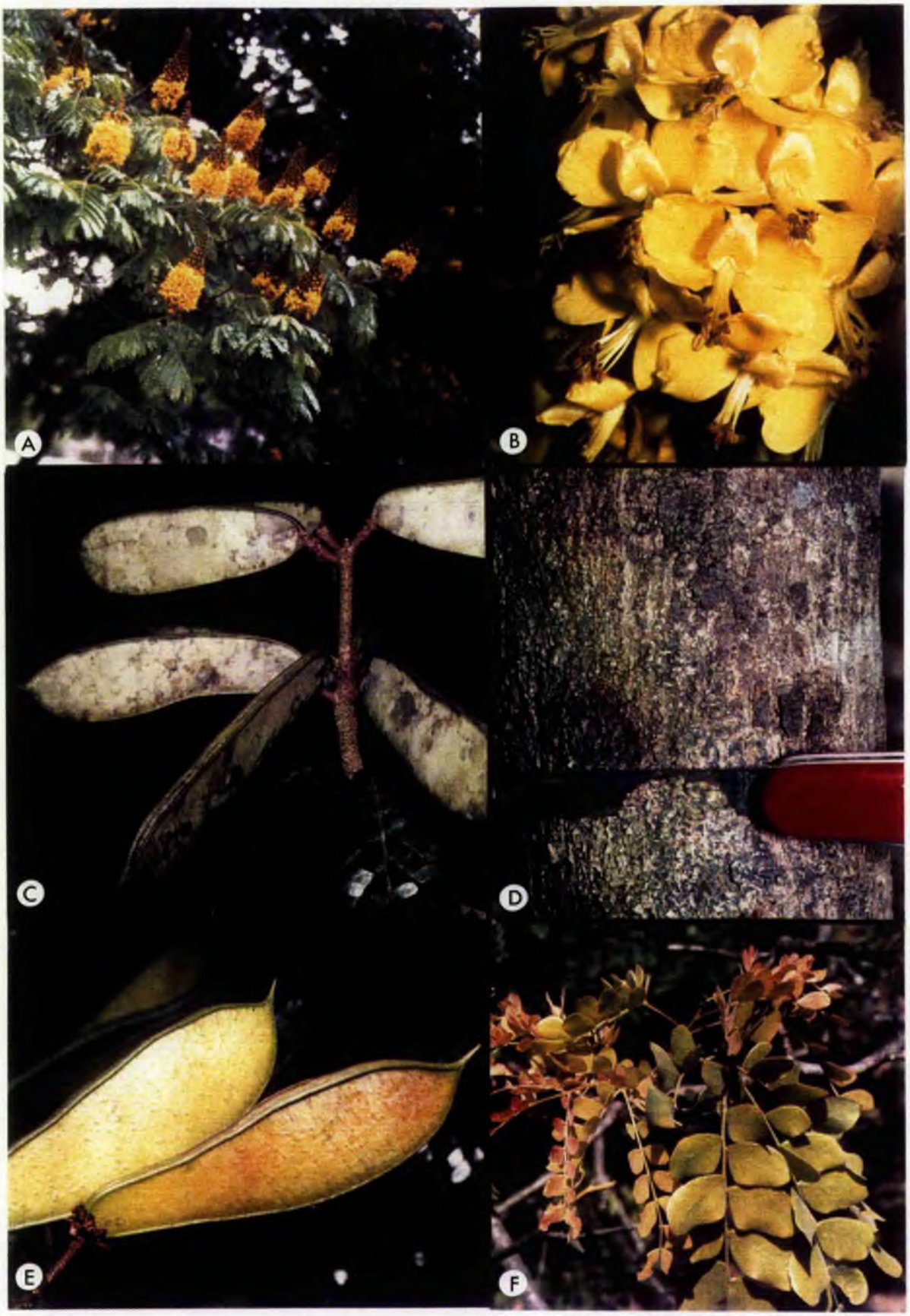


FIG. 52. *Caesalpinia pluviosa* var. *peltophoroides*: **A** flowering branch, cultivated tree in Boa Vista, Brazil (unvouchered; photo: A. Patterson); **B** flowers, cultivated tree in Linhares, Brazil (unvouchered); **C** fruits (*Lewis et al.* 1632); **D** bark, cultivated tree in Linhares (unvouchered); *C. pluviosa* var. *cabraliana*: **E** fruits (*Lewis et al.* 2019); *C. pluviosa* var. *sanfranciscana*: **F** young flush foliage, Bahia, Brazil (unvouchered).

BRAZIL. Amazonas, Manaus (cult.), 24 Aug. 1980, *Lowe* 3951 (K!); Manaus (cult.), 26 Sept. 1973, *Silva* 1842 (INPA!, NY!); **Roraima**, Boa Vista (cult.), 4 April 1987, *Lewis* 1604 (E!, K!); **Distrito Federal**, Brasília (cult.), 4 Dec. 1982, *Castelo* 18 (NY!); Brasília (cult.), 16 May 1980, *Castro* 3 (UB!); Brasília (cult.), 26 April 1972, *Heringer* 12103 (UB!); **Mato Grosso**, Cuiabá (cult.), 4 Feb. 1986, *Lewis* s.n. (K!); Chapada dos Guimarães (cult.), 22 Oct. 1973, *Prance et al.* 19304 (INPA!, K!, NY!, US!); **Minas Gerais**, Belo Horizonte (cult.), 8 March 1937, *Barreto* 6562 (F!); Belo Horizonte (cult.), 27 Aug. 1937, *Barreto* 7745 (F!, UB!); Belo Horizonte (cult.), 4 Jan. 1959, *Irwin* 2371 (F!, K!, NY!); estação experimental Agua Limpa, 14 Dec. 1965, *Monteiro* s.n. (RB 130234) (RB!); **Bahia**, Itajuípe, 24 Nov. 1966, *Belém & Pinheiro* 2916 (NY!, UB!); Mun. Itabuna, faz. Sto. Antonio (cult.), 28 Oct. 1983, *Callejas et al.* 1562 (K!, NY!); Salvador (cult.), 11 March 1940, *Dahlgren* s.n. (F!); Mun. de Ilhéus, CEPEC (cult.), 25 Oct. 1978, *Mattos Silva & Hage* 209 (K!); Mun. de Ilhéus, faz. Theobroma, 30 April 1989, *Mattos Silva* 2732 (K!); Mun. Santa Cruz Cabrália, Estação Ecólogica Pau Brasil, 39°08'W, 16°23'S, 16 Oct. 1987, *Santos* 645 (K!); **Espirito Santo**, Linhares, Reserva florestal, CVRD, c 40°W, 19°30'S (cult.), 13 May 1987, *Lewis et al.* 1632 (K!, RB!); **Rio de Janeiro**, Rio (cult.), Oct. 1920, *Constantino* 13377 (K!); 18 Nov. 1864, *Glaziou* 6 (BR!); Oct. 1873, *Glaziou* 6838 (K!); *Glaziou* 1032 (BR!, F!); *Glaziou* 11905 (BR!, F!, K!); *Glaziou* 12609 (K!); 8 Oct. 1872, *Glaziou* 6187 (E!); 10 Sept. 1962, *Martins* 279 (F!, GH!, K!); Nov. 1835, *Riedel* s.n. (NY!); **Paraná**, Londrina (cult.), 30 Sept 1985, *Dias* s.n. (UEC!); Mun. Dois Vizinhos, Foz do Chopim, Nov. 1974, *Hatschbach & Pelanda* 40736 (MBM!); **São Paulo**, São Paulo (cult.), 23 Oct. 1962, *Pabst* 7140 (K!, M!, NY!); São Paulo (cult.), 10 Dec. 1968, *Pabst* 9281 (HBG!, K!); **COLOMBIA**. Dept. Valle, Cali (cult.), 27 April 1990, *Silverstone-Sopkin* 5960 (CUVC!, K!); Cali (cult.), 26 Feb. 1990, *Silverstone-Sopkin* 5953 (CUVC!, K!); **BOLIVIA**. Depto. Santa Cruz, city of Santa Cruz (cult.), 2 Oct. 1981, *Beck* 7155 (NY!).

ECOLOGY. Thought to be native in coastal forests of eastern Brazil, from southern Bahia to the state of Rio de Janeiro but nearly all herbarium specimens come from cultivated street trees, 50--800 m (Brazil).

PHENOLOGY. Flowering August to May, fruiting October to May.

VERNACULAR NAMES. "Sibipiruna" (Brazil) and numerous orthographic variants of this, e.g.: "Sebipira", "Sepipiruna", "Sepipiraúna", "Sibipurana" and "Sibipiruma"; "Pirapitá" (Bolivia).

NOTES. *C. pluviosa* var. *peltophoroides* apparently lacks stellate or plumose hairs on the inflorescence rhachis but red, stipitate glands on the leaf rhachis have hairy stalks - a feature not found on *C. pluviosa* var. *pluviosa*. *Beck* 7155, a cultivated specimen of var. *peltophoroides* from Bolivia appears similar to *Michel* 155 a specimen of var. *pluviosa*, also from Bolivia, but has flowers in racemes, buds with a darker indumentum, lacks

plumose hairs on the inflorescence rhachis and has smaller leaflets with subepidermal idioblasts less evident.

C. pluviosa var. *peltophoroides* appears to be closely related to *C. eriostachys*, a widespread species in Mexico and Central America, but the flowers of the former are more closely packed on the inflorescence rhachis and the plant lacks stellate hairs (although the plumose or dendritic hairs are similar). The thecal bridge on the anthers of *C. pluviosa* var. *peltophoroides* is paralleled by apical glands on the anther thecae of *C. eriostachys*. *C. pluviosa* var. *peltophoroides* flowers when in full leaf whereas *C. eriostachys* usually flowers when leafless or almost so.

Stipules in the *C. pluviosa* 'complex' are poorly-known being early caducous. Those observed on var. *peltophoroides* are foliaceous, c 4 mm long and have a fimbriate margin. Red, pubescent, stipitate glands are often clustered in the axes of the leaflet pulvinules. Sometimes a distinct colour contrast can be noted above and below the point of articulation on the pedicels. The flowers are noted as being strongly scented with a perfume not unlike that of vanilla (*Martins* 279, *Lewis* 1604).

33d. var. **cabraliana** *G.P. Lewis* var. nov., in sched. Type: Brazil, Bahia, Mun. de Santa Cruz de Cabrália, c 12 km NW of Porto Seguro, 27 Nov. 1979, *Mori et al.* 13029 (holotype CEPEC!, isotypes K!, NY).

Leaf rhachis 4.5--8 cm long, pinnae in 5--6 pairs plus a terminal pinna, leaflets in 18--22 pairs per pinna, terminal leaflets 8--12 x 4--7 mm, inflorescence a panicle, stamen filaments 13--15 mm long. (Figs. 1E & 52E, Map 18).

DISTRIBUTION. Endemic to the region around Santa Cruz Cabrália in SE Bahia, Brazil.

BRAZIL: Bahia, Mun. de Santa Cruz Cabrália, c 16 km W of Porto Seguro, Estação Ecológica do Pau Brasil, 8 May 1991, *Lewis et al.* 2019 (CEPEC!, K!); same locality, 20 May 1987, *Lewis & Mourão* 1644 (K!, RB!); same locality, 3 April 1979, *Mattos Silva et al.* 324 (US!); 3 km NE of Estação Ecológica Pau Brasil, 27 Nov. 1979, *Mori et al.* 13029 (holotype CEPEC!, isotype K!); Estação Ecológica Pau Brasil, 23 Aug. 1983, *Santos* 14 (CEPEC!); same locality, 7 May 1984, *Santos* 330 (CEPEC!); same locality, 10 Feb. 1989, *Santos* 930 (K!); same locality, 7 Dec. 1989, *Santos* 727 (CEPEC!).

ECOLOGY. Moist coastal forest, 40 m.

PHENOLOGY. Flowering from November to February, fruiting from March to May with fruits persisting until August.

VERNACULAR NAME. "Mucitaiba".

NOTES. The fruits of this variety have characteristic markings on their valves, these are small dashes which are orientated more or less at right angles to the pod margins or are randomly scattered in several directions. They have, so far, not been observed on the fruits of any other variety of *C. pluviosa*. The blackish brown bark of mature trees breaks away from the trunk in thick, rectangular chunks, the inner bark is pea green and the slash whitish cream. Stipitate glands noted on the stems and leaf rhahides of seedlings (*Lewis & Mourão* 1644) are lacking on mature foliage.

33e. var. **paraensis** (*Ducke) G.P. Lewis*, stat. and comb. nov., in sched.

Caesalpinia paraensis Ducke in Archiv. Jard. Bot. Rio de Janeiro 4: 59 (1925). Type: Brazil, Pará, near Monte Alegre, *Ducke* s.n. (isotypes BM! [MG Herb No. 16053], K! [RB Herb. No. 17020], MG [Herb No. 16053], RB [Herb. No. 17020]).

Leaf rhachis 2--11 cm long, pinnae in 2--5(--6) pairs plus a terminal pinna, leaflets 12--16 per pinna, terminal leaflets 12--28 x 9--16 mm, inflorescence a panicle, stamen filaments c 10 mm long. (Fig. 1F, Map 18).

DISTRIBUTION. Brazil, in Pará (restricted to the area around Monte Alegre), south eastern Bahia, north eastern Minas Gerais and the area around Cabo Frio in Rio de Janeiro state.

BRAZIL: Pará, Monte Alegre, 4 March 1923, *Ducke* 17020 (K!); Rio Maicurú, mun. de Monte Alegre, 16 Sept. 1953, *Froes* 30251 (RB!); **Bahia**, Juçaré, 27 May 1966, *Belém & Pinheiro* 2312 (CEPEC!, NY!, RB!, UB!); Juçaré, 27 May 1966, *Belém & Pinheiro* 2332 (NY!); Itamerim, 28 Dec. 1965, *Pinheiro* 4 (UB!); Itabuna, Juçaré, 18 July 1967, *Pinheiro* 118 (CEPEC!); Itajú do Colonia, 23 Jan. 1969, *dos Santos* 345 (CEPEC!); Itororó, road to Rio do Meio, 13 Jan. 1971, *dos Santos* 1306 (US!); **Minas Gerais**, Itinga to Pedra Azul, 23 Nov. 1964, *Duarte* 8564 *& Pereira* 9334 (NY!); **Rio de Janeiro**, Ilha de Cabo Frio, without date, *Capanema* s.n. (RB No. 5129) (RB!); Mun. de Cabo Frio, Búzios, 5 Jan. 1982, *Claudio* 45 (RB!);

Búzios, 5 Jan. 1982, *Collares* 105 (RB!); new road to Búzios, Baia Formoso, 8 May 1987, *Lewis et al.* 1629 (K!, RB!); *Lewis et al.* 1628 (K!, RB!); Rio de Janeiro, ?1832, *Riedel & Luschnath* 2170 (RB!); Aldeia de São Pedro, near Cabo Frio, Sept. 1881, *Schwacke* 3090 (RB!); Cabo Frio, Praia do Pero, 22 Jan. 1967, *Sucre* 1438 (RB!); Cabo Frio, 17 Jan. 1967, *Sucre* 1354 (RB!); Cabo Frio, 17 Dec. 1966, *Sucre* 1311 (RB!).

ECOLOGY. Arboreal restinga on sandy soil; deciduous forest; or medium density, low altitude, humid forest on red clays or stony soils, 10--70 m.

PHENOLOGY. Flowering from November to March and sometimes to May or even July, fruiting from January through to July.

VERNACULAR NAMES. "Muirapixuna" (Pará), "Sucupira" (Bahia), "Mucutaibo-preto" (Bahia).

NOTES. Juvenile foliage usually displays a pinkish flush. The stipules are linear to broadly spathulate, c 4--7 mm long, fimbriate, pubescent, glandular and early caducous. Leaflet size is very variable, especially on regrowth branchlets of coppiced specimens. Plumose or dendritic trichomes on young shoots are similar to those of var. *intermedia*. The disjunct distribution of var. *paraensis* requires further study.

33f. var. **sanfranciscana** *G.P. Lewis* var. nov., in sched. Type: Brazil, Bahia, 35 km S of Livramento do Brumado, 1 April 1991, *Lewis & Andrade* 1932 (holotype CEPEC!, isotypes K!).

Leaf rhachis 1.5--5.2 cm long, pinnae in 2--4 pairs plus a terminal pinna, leaflets 9--13(--17) per pinna, terminal leaflets 20--33 x 10--18 mm, inflorescence a panicle, stamen filaments 15--17 mm long. (Figs. 2B, 52F & 53, Map 18).

DISTRIBUTION. Brazil, endemic to central Bahia and northern Minas Gerais, princiapally in the São Francisco river basin.

BRAZIL: Bahia, Mun. Livramento do Brumado, c 30 km along road from Brumado to Livramento do Brumado, 12 March 1991, *Brito & Lewis* 288 (K!); Mun. de Bom Jesus da Lapa, c 8 km along road Lapa to Ibotirama, without date, *de Carvalho et al.* 1806 (K!); km 10 along road Paratinga to Bom Jesus de Lapa, 1 July 1983, *Coradin et al.* 6331 (CEPEC!, K!, NY!, SI!); 22.6 km SE of Xique-Xique on BA-052 road to Irecê, 28 Feb. 1977, *Harley et al.* 19165 (K!); Chapada Occidental da Bahia, 37 km SE of Correntina, on road to Jaborandi, 24 April 1980, *Harley et al.* 21695 (CEPEC!); Basin of Upper São Francisco River, c 28

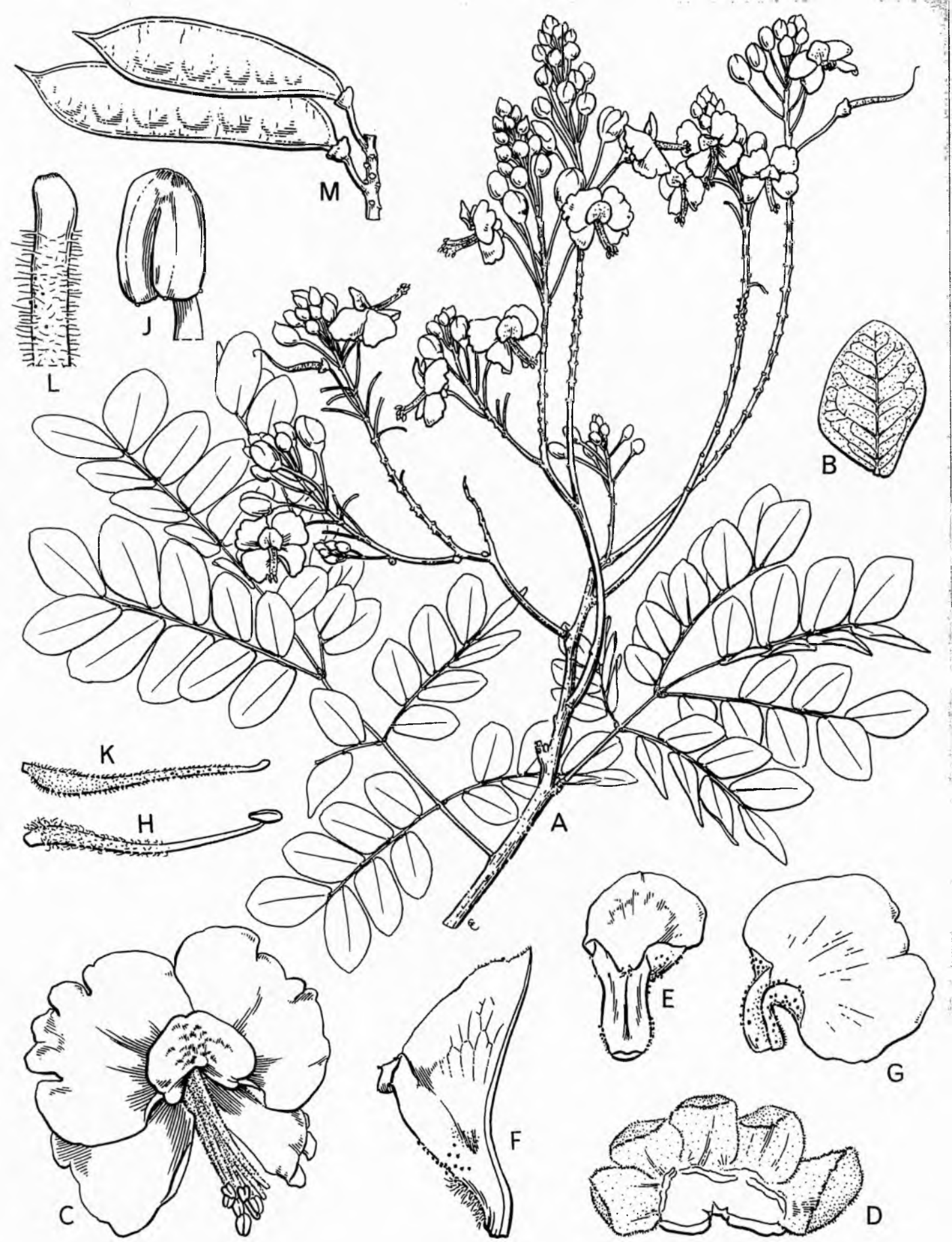


FIG. 53. *Caesalpinia pluviosa* var. *sanfranciscana*. **A** inflorescence and foliage x ¾; **B** leaflet undersurface x 1½; **C** flower x 3; **D** calyx opened out x 2¼; **E** standard petal x 3; **F** l.s. standard petal x 6; **G** upper lateral petal x 3; **H** stamen x 3; **J** anther x 18; **K** gynoecium x 3; **L** style apex and stigma x 18; **M** fruit x ¾. **F** from *Lewis & Andrade* 1862, **M** from *Lewis & Andrade* 1896, the rest from *Lewis & Andradè* 1932. Drawn by Eleanor Catherine.

km SE of Bom Jesus da Lapa on road to Caetité, 16 April 1980, *Harley et al.* 21409 (K!, NY!); 20 km S of Livramento do Brumado, 20 March 1991, *Lewis & Andrade* 1865 (CEPEC!, K!, RB!); 35 km S of Livramento do Brumado, 1 April 1991, *Lewis & Andrade* 1932 (holotype CEPEC!, isotype K!); 10 km S of Livramento do Brumado, 26 March 1991, *Lewis & Andrade* 1896 (CEPEC!, K!); 20 km S of Livramento do Brumado, 20 March 1991, *Lewis & Andrade* 1862 (CEPEC!, K!, MEXU!, NY!, SI!); 10 km S of Livramento do Brumado, 26 March 1991, *Lewis & Andrade* 1892 (CEPEC!, K!); 40 km along road from Livramento do Brumado to Brumado, 12 March 1991, *Lewis et al.* 1857 (CEPEC!, K!, MEXU!, NY!); 35 km S of Livramento do Brumado, 13 March 1991, *Lewis et al.* 1860 (CEPEC!, K!, MEXU!, NY! SI!); Cruz das Almas (seeds originally from Paratinga), 4 Feb. 1981, *Pinto* 43/81 (CEPEC!); **Minas Gerais**, Rio Pandeiros, c 52 km W of Januária, nr. road to Serra das Araras, 21 April 1973, *Anderson* 9306 (NY!); 22 km W of Januária on road to Serra das Araras, 19 April 1973, *Anderson* 9201 (US!); Mun. Janaúba, Ribeirão Poções, 13 Nov. 1991, *Hatschbach et al.* 55097 (K!).

ECOLOGY. In various forms of deciduous forest, especially along the margins of seasonal rivers in caatinga; open slope forest with cacti, calcareous and quartzite outcrops, 400--610 m.

PHENOLOGY. Flowering November to April, fruiting February to April and sometimes into July.

VERNACULAR NAME. "Catingueira".

NOTES. The variety has a facies similar to that of *C. pyramidalis* but differs noticeably in having paniculate inflorescences and flowers with pedicels that are articulated just below the calyx. *Lewis & Andrade* 2005 and 2008 are possibly the result of natural hybridization between var. *sanfranciscana* and *Caesalpinia laxiflora*. *C. pluviosa* var. *sanfranciscana* has smooth or rough grey bark with numerous lenticels; the outer bark slash is orangish brown, the inner slash creamish. The hard heartwood is dark brown. Stipules are linear-lanceolate to broadly spathulate, c 3 mm long, densely glandular, pubescent near the base, ciliate on the margins, and are early caducous.

34. **Caesalpinia echinata** *Lam.*, Enc. Meth. Bot. 1: 461 (1785). Type: Brazil (holotype P, n.v.).

Guilandina echinata (Lam.) Spreng., Syst. 2: 327 (1825).

Caesalpinia vesicaria Vell., Fl. Flum.: 172 (1825), Ic. 4, tab. 89 (1835). ("*vessicaria*"), non L. (1753).

Caesalpinia obliqua Vogel in Linnaea 11: 407 (1837). Type: Brazil, *Sellow* s.n. (holotype ? B†).

Armed tree, c 5--15 m+, DBH 15--40 cm; bark dark brown to black with greyish, pustular lenticels, bark flaking in large woody sheets; young branchlets with round, pustular lenticels pushing through greyish, pubescent bark to reveal a dark red underbark (the outer bark thus vertically fissured) stems with upturned, 1--2 mm long thorns arising from woody protuberances, these lacking on more mature specimens and larger branches; young stems finely tomentellous, glabrescent. *Leaves* bipinnate; stipules early caducous, on seedlings lanceolate, acute to acuminate, pubescent, striate caducous, a pubescent, lanceolate-triangular, persistent, 0.25--0.5 mm long stipel below the pulvinus of each leaflet on the lower surface of the pinna rhachis; petiole 0.8--2.5 cm long; rhachis 3--8(--15) cm long, tomentellous; pinnae 4--10 per leaf, alternate or the terminal two opposite; leaflets coriaceous, 9--19 per pinna, alternate, increasing or decreasing in size towards pinna apex, broadly oblong to subrhombic, apex rounded to obtuse to emarginate, base subtruncate, asymmetric, terminal leaflets 1.1--2.7(--5) x 0.5--2(--3.6) cm, medians 0.9--3(--4.5) x 0.6--1.6(--3) cm, both surfaces nitid, essentially glabrous or the margins ± ciliate and the midvein on both surfaces finely tomentellous; midvein excentric, secondary veins brochidodromous, tertiary veins reticulate; blades appearing eglandular although red, subepidermal glands are usually present. *Inflorescence* a 15--40-flowered terminal (or rarely axillary) raceme or few-branched panicle, finely tomentellous, especially on the calyces; bracts broadly ovate-triangular, acute to acuminate, under 1 mm long, tough and coriaceous, pubescent especially on the basal $^1/_2$, early caducous; pedicels (6--)9--18 mm long, articulated 1.5--4 mm below calyx. *Calyx* lobes 5--7.5 mm long, the lowest slightly cucullate, c 7--9 mm long, all with both surfaces pubescent and margins ciliate, all reflex or inroll post anthesis. *Corolla* yellow; standard petal with a blood red blotch or mostly deep carmine with a yellow apex, ± spathulate, 11--13 x 4--7 mm (including a claw of up to c 5 mm), basal 2 mm of claw densely pubescent on the margin and with a small tuft of white hairs on the inner surface about 1.5 mm from its base; upper lateral petals broadly obovate-rectangular, 11--13 x 7--10 mm (including a 0.25--1 mm claw), apex shallowly emarginate, claw moderately pubescent on margins and inner surface; lower laterals broadly obovate, 11--15 x 7--9 mm (including a 0.25--1 mm claw), claw sparsely

pubescent on inner surface and margins, all petals eglandular. Stamen filaments 7--9 mm long, bases somewhat expanded, vexillary stamen with a short stipe, all pubescent on basal $^1/_2$--$^2/_3$; anthers 0.75--1 x 0.5 mm. Ovary pubescent with small spines intermixed; style 4--5 mm, apically expanded; stigma a subterminal, fringed chamber. *Fruit* a sublunate, dehiscent, woody, 1--2-seeded pod, 5.5--7.3 x 1.9--2.6 cm (including a stipe of 2--4 mm), valves twist after dehiscence, surfaces finely pubescent with 5 mm long woody spines intermixed, young spines hairy. Mature seeds not seen. *Seedling* germination phaneroepigeal, first and second eophylls opposite, pinnate, each pinna with 4--5 pairs of opposite leaflets, blades elliptic-oblong, apex apiculate-mucronate, base asymmetric, auriculate on proximal side, a lanceolate, gland-tipped, sparsely pubescent stipel below each leaflet pulvinule, third eophyll with 1(--2) pairs of opposite pinnae, each pinna with 7 alternate leaflets. (Figs. 5L, **54** & 55, Map 19).

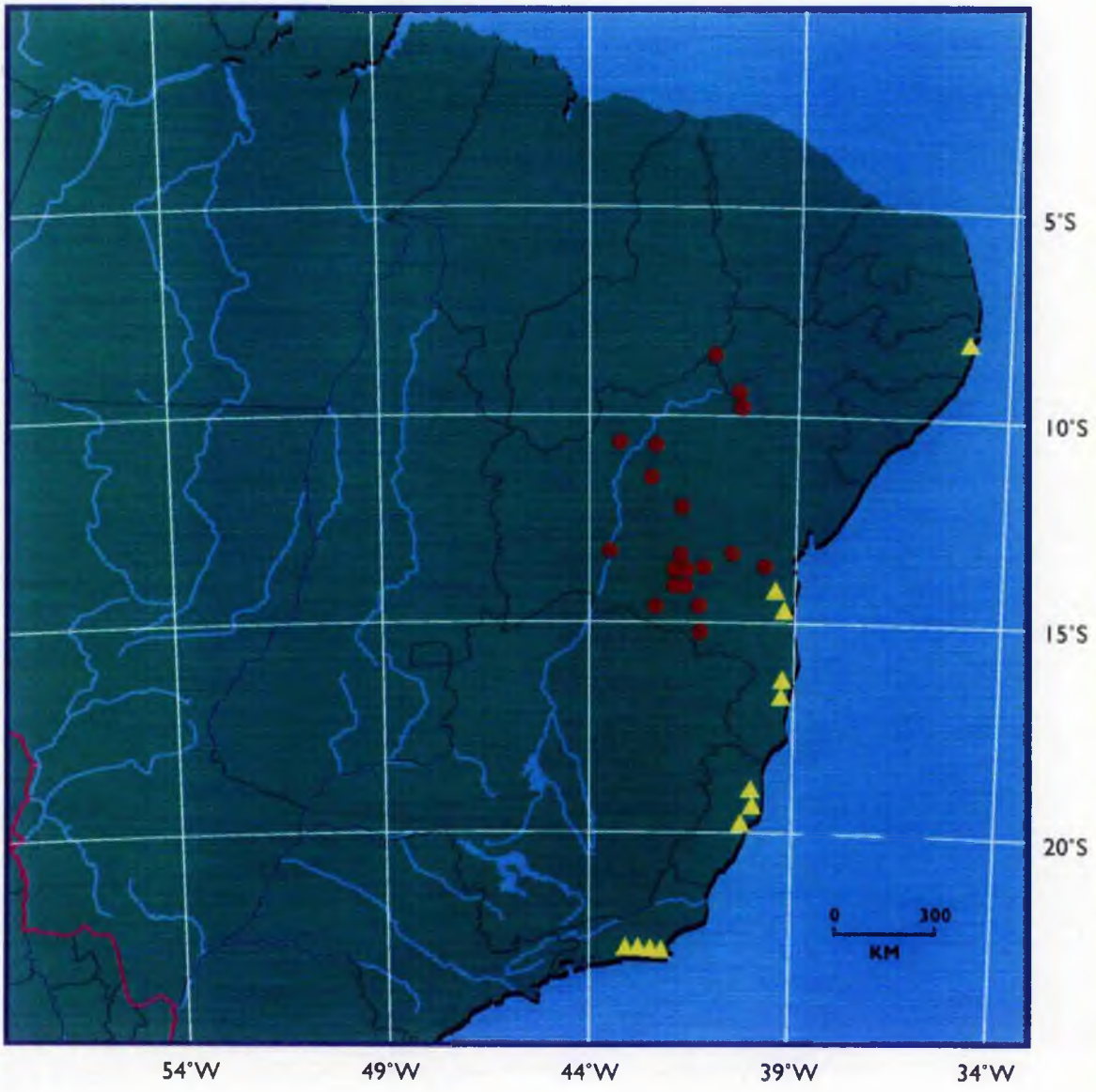
DISTRIBUTION. A native of eastern Brazil, still extanct in the states of Pernambuco, Bahia, Espirito Santo and Rio de Janeiro. In herbaria mostly known from cultivated material.

BRAZIL: Pernambuco, Tapera, 23 Jan. 1932, *Pickel* 2893 (F!, GH!); **Bahia**, Mun. de Porto Seguro, BR 101 road from Itabela to Trancoso, 18 May 1987, *Lewis & Mourão* 1639 (K!, RB!); **Espirito Santo**. Mun. de Aracuz, nr. Linhares, Guaraná, Sept. 1978, *Horst* 3 (K!); **Rio de Janeiro**, without exact locality or date, *Allemão* s.n. (BR!); nr. Rio de Janeiro, without date, *Burchell* 2825 (K!); Rio de Janeiro, 4 Oct. 1873, *Glaziou* 6839 (BR!, K!, MG!); Mun. de Cabo Frio, new road to Búzios, Bahia Formoso, 8 May 1987, *Lewis et al.* 1626 (K!, RB!); Mun. São Pedro d'Aldeia, São Mateus, 7 May 1987, *Lewis et al.* 1624 (K!, RB!); Mun. de Saquarema, Saquarema, 5 May 1987, *Lewis et al.* 1622 (K!, RB!); same locality and date, *Lewis et al.* 1621 (K!, RB!); Mun. de Cabo Frio, near Barra Morro do Farol, 29 Aug. 1986, *de Lima et al.* 2690 (K!, NY!); near Sebastianopolis, Aug. 1817, *Martius* s.n. (M!); **without locality in Brazil**, without date, *Sellow* s.n. (E!, K!); 1829, *Princeps Maximilianus Neovidensis* s.n. (BR!); **Cultivated material: Pará**, Belém, 4 Oct. 1957, *Cavalcante* 305 (F!, MG!); **Pernambuco**, Recife, March 1993, *Guerra* s.n. (K!); **Alagoas**, Maceió, 31 March 1981, *de Lyra* 233 (HRB!, MO!, NY!); **Bahia**, Salvador, 1940, *Dahlgren* s.n. (F!); Ubaitaba, cocoa plantation, 8 March 1966, *Pinheiro* 71 (UB!); Mun. Santa Cruz Cabrália, Estação Ecólogica do Pau-Brasil, c 16 km W of Porto Seguro, 8 Dec. 1987, *Santos* 754 (K!); Ipiaú, road to Ibirataia, cocoa plantation, 30 Oct. 1970, *dos Santos* 1239 (NY!, RB!); **Minas Gerais**, Viçosa, 21 Nov. 1980, *de Silva Ramalho* 1997 (RB!); **Espirito Santo**, Linhares, Reserva Florestal de CVRD, 14 May 1987, *Lewis et al.* 1634 (K!, RB!); Reserva Biologica de Sooretama, N of Linhares, 14 May 1987, *Lewis et al.* 1635 (K!, RB!); same locality, Aug. 1965, *Lanna Sobrinho* 1135 (F!); **Rio de Janeiro**, Tijuca, 12 Oct. 1960, *Angeli* 201

FIG. 54. *Caesalpinia echinata*. **A** inflorescence and foliage x 1; **B** leaflet undersurface x 1½; **C** examples of bark thorns, front and side views x 1½; **D** flower x 3; **E** l.s. flower x 3½; **F** standard petal x 4½; **G** upper lateral petal x 4½; **H** lower lateral petal x 4½; **J** stamen x 9; **K** gynoecium x 9; **L** stigma x 15; **M** fruit x 1; **N** twisted fruit valve x 1; **P** seedling x 1. **A** from *Glaziou* 6839, **B** & **L** from *Angeli* 201, **C** & **N** from *Lewis et al.* 1634, **D** from *Lima et al.* 2705, **E–K** from *Ducke* 20623, **M** from *Mell* s.n., **P** from *Lewis et al.* 1624. Drawn by Tim Galloway.

FIG. 55. *Caesalpinia echinata*: **A** flowers, cultivated tree in Rio de Janeiro Bot. Gard. (photo.: H.C. de Lima); **B** red exudate from trunk (*Lewis et al.* 1641); **C** habit of largest variant (*Lewis et al.* 1622); **D** fruits, Espirito Santo (unvouchered); **E** violin bows made from "pau brasil", Espirito Santo; **F** seedling of variant with medium-sized leaflets, cultivated Espirito Santo.

Distribution of *Caesalpinia echinata* (△) and *C. laxiflora* (●) in Brazil



(K!); Nov. 1928, *Ducke* 20623 (MO!); Botanic Garden Rio, 9 Oct. 1986, *de Lima et al.* 2705 (K!, NY!); 8 Nov. 1978, *de Lima* s.n. (RB!); **Distrito Federal**, Botanic Garden Brasília, 9 Dec. 1985, *Equipe de JBB* 639 (UEC!); Brasília, Parque do Guará, 14 Nov. 1972, *Heringer* 12240 (UB!); Brasília, 16 March 1978, *Heringer* 16969 (NY!, UEC!, US!); Brasília, 10 Sept. 1981, *Machado* 047 (UB!); **TRINIDAD**, Botanic Garden, 11 March 1889, *Hart* 3574 (K!); Port of Spain, 12 July 1927, *Mell* s.n. (NY!).

ECOLOGY. Disturbed, dry coastal cactus scrub with rocky outcrops (as a small contorted tree), inland in mata atlantica (as a large tree), tall restinga on well-drained sandy soil. Commonly cultivated as an ornamental street or park tree.

PHENOLOGY. Flowering and fruiting from as early as the end of August through to March.

VERNACULAR NAMES. "Ibirapitanga", "Pau Brasil".

NOTES. Presently *Caesalpinia echinata* is not segregated into infraspecific taxa although several populations show marked differences in leaflet shape and size, wood colour and general habit. These populations are under study by Cavalcante de Lima and co-workers and in due course subspecies or varieties of *C. echinata* may be recognised. So far, three morphologically distinct groups have been detected. The most common form, with smaller leaflets and an orangish-chestnut coloured heartwood, is known from several localities along the Brazilian coast. The second form differs but slightly from the first, having larger leaflets and a reddish-orange heartwood. Specimens of this second variant are only known in cultivation in the Biological Reserve of Sooretama in Espirito Santo and in the Rio de Janeiro Botanical Gardens. *Lewis et al.* 1635, for example, from Sooretama is a collection with particularly large leaflets, the terminals attaining 6.4 x 4.5 cm. *Sobrinho* 1135, from the same locality, and *Horst* 3 from the municipality of Aracuz, near Linhares in Espirito Santo also have the larger leaflets typical of the Espirito Santo material. The third form has very large leaflets, up to 12 cm long, and blackish-red wood and is known from a population in the municipality of Eunápolis in Bahia. Specimens of this form are being cultivated in the Rio Botanical Gardens. (Cavalcante de Lima, 1992).

The country Brazil was named after "pau brasil" and there is a long and complicated history surrounding the species and its exploitation, especially for the extraction of a red dye and for durable timber. Brazilian indians used the wood to make various weapons, and today the wood is still exported, sometimes illegally, to Europe for the manufacture of high quality violin bows. The species has been used as an ornamental in parks and gardens

but grows too slowly to be of use along modern public highways. It has occasional medicinal uses, as an astringent, a tonic or an antidiuretic. Ramalho (1978) reports that the boiled bark cures diarrhoea and dysentry, and a powder made from the bark is a tonic for the gums. An extract of the wood is being tested as a treatment of cancerous tumors, with encouraging results. (Cavalcante de Lima, 1992).

Various workers have erroneously suggested that *C. echinata* belongs to subgenus *Guilandina* because of its spiny fruits, but in Brazil it belongs to section *Caesalpinaria* which in this treatment falls within the broadened concept of *Poincianella*. By its distinctive flower colour, spiny fruits and armed stems and branches it is easily distinguishable from all other neotropical species of *Caesalpinia sens. lat.* Its flowers are usually highly perfumed and their colour, morphology and size suggest bee pollination.

35. **Caesalpinia calycina** *Benth.* in Mart. Fl. Bras. 15(2): 71 (1870). Type: Brazil, Bahia, near Rio de Contas, March 1817.
Prinz zu Wied-Neuwied (Princeps Maximilianus Neovidensis) s.n. (holotype BR!).

Unarmed, single or multiple-stemmed shrub, 2--4 m tall; stems 1.5--2 cm diam., bark reddish brown or greyish brown, papery, peeling and splitting vertically to reveal dark green under-bark with numerous white lenticels; branchlets finely puberulous, densely stipitate-glandular with pixie-cup glands, the gland stalks puberulous. *Leaves* bipinnate; stipules broadly ovate-orbicular, apex rounded, base cordate, 6--7 x 6 mm, puberulous, stipitate-glandular, margin fimbriate, the fimbriae gland-tipped, semi-persistent; petiole 4--6.8 cm long, sparsely pubescent, glabrescent, stipitate, pixie-cup glands intermixed with pubescence; rhachis 4.8--14.5 cm long, as for petiole; pinnae in 3--6 opposite pairs plus a terminal pinna (or this lacking); leaflets in 10--12 opposite pairs, oblong-elliptic, terminal leaflets 9--11 x 3--4 mm, medians 12--18 x 3.5--6 mm, both surfaces glabrous but for a few small hairs at base on margin and pulvinule, blade fleshy, the venation obscure, excentric main vein visible on lower surface; black punctate glands along leaflet margin on lower surface, the margin sometimes crenulate, especially near the apex; juvenile foliage with a corona of triangular-lanceolate, gland-tipped, stipel-like appendages clustered around the pinnae insertions. *Inflorescence* a 20--75-flowered terminal or axillary raceme,

rhachis, pedicels and calyces finely puberulous and densely glandular with short-stalked, red pixie-cup glands; bracts ovate-lanceolate, acuminate, falcate, 15 x 7 mm, puberulous, densely pixie-cup glandular, margins fimbriate, the fimbriae gland-tipped; pedicels 6--6.5 mm long, not articulated. *Calyx* lobes 12--15 mm long, the lowest cucullate lobe longest, finely puberulous, stipitate-glandular (except where lobes have overlapped in bud). *Corolla* golden yellow; standard with a few orange markings near apex or more usually these lacking, blade subpanduriform, basal $^2/_3$ thickened, infolded and suborbicular, apical $^1/_3$ flimsy, reflexed and narrower, c 16--17 x 12 mm (including a 1.5--3 mm claw), outer surface of claw and basal $^2/_3$ of blade short-stalked glandular, claw glabrous and lacking apical ridges or flanges; upper lateral petals broadly elliptic, 18--20 x 15--16 mm (including a 1 mm claw), lower laterals elliptic,18--19 x 13 mm (including a 1 mm claw), all 4 laterals with outer surface of claw and blade base, just above claw, glandular, claw inner surface pubescent. Stamen filaments pale yellow, 2.2--2.4 cm long, basal $^1/_3$ densely pubescent, some filaments of each flower with a few short-stalked glands at base on upper surface; anthers pink, becoming red with age, 2--2.5 x 1--1.5 mm. Ovary pubescent, glandular, up to 7-ovulate; stigma a terminal, fringed chamber. *Fruit* a thinly woody, explosively dehiscent pod, 8.5--10.5 x 1.7--2.2 cm, valves finely puberulous and moderately stipitate-glandular, 3--6-seeded. *Seeds* cordate to broadly ovate-triangular, 9--10 x 9--10 x 2 mm, brown or orangish ochre-brown, sometimes overspeckled dark brown, shiny. Seedling germination phaneroepigeal, cotyledons foliaceous, first eophyll pinnate with 5 opposite pairs of leaflets, second eophyll alternate to first, bipinnate with one pair of opposite pinnae plus a terminal pinna, each with 4--5 opposite leaflet pairs, all leaflets with red, submarginal glands on lower surface, stipules ovate, fimbriate and persistent, hypocotyl glabrous and glandular, epicotyl pubescent and stipitate-glandular, the short gland stalks pubescent. (Figs. 2C, 8A, 9F & 56, Map 17).

DISTRIBUTION. Brazil in the states of Bahia and Pernambuco.

BRAZIL: Pernambuco, between Cabrobó and Murici, 15 May 1971, *Heringer et al.* 765 (RB!, UB!); **Bahia**, Mun. de Don Basílio, c km 60 along road from Brumado to Livramento do Brumado, 13 March 1991, *Brito & Lewis* 300 (CEPEC!, K!); c 52 km along road Brumado to Livramento do Brumado, 28 Dec. 1989, *de Carvalho* 2693 (CEPEC!, K!); 11--12 km S of Livramento do Brumado, 23 Nov. 1988, *Harley et al.* 26985 (K!); 10--15 km W of Contenda do Sincorá, 22 Dec. 1985, *Hatschbach & Silva* 50081 (K!); same

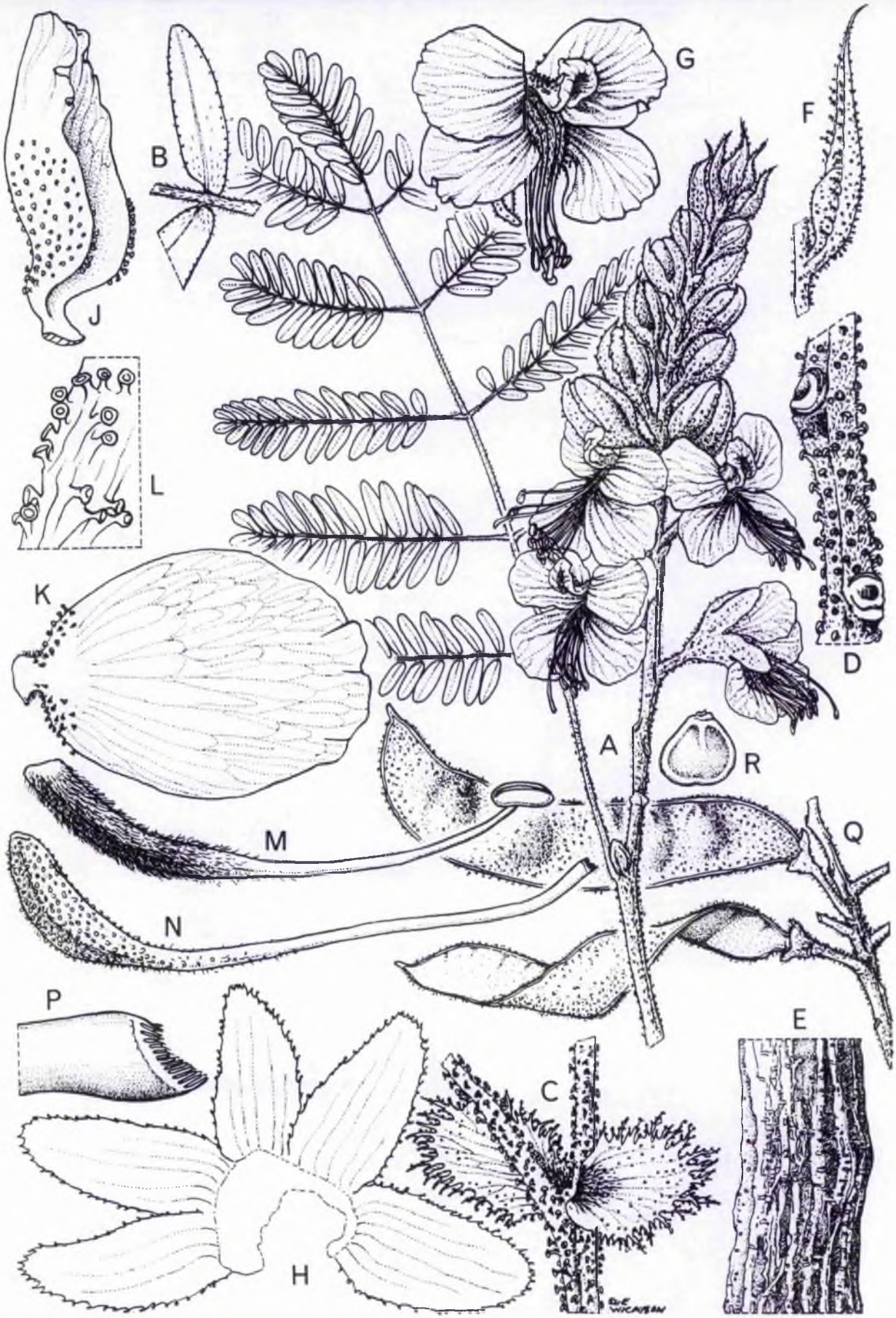


FIG. 56. *Caesalpinia calycina*. **A** inflorescence and part bipinnate leaf x 1; **B** median leaflets undersurfaces x 3; **C** stipules x 4½; **D** glands on stem x 6; **E** stem bark x 1½; **F** bud enclosed by bract x 3; **G** flower x 1½; **H** calyx opened out x 3; **J** standard petal x 4½; **K** lateral petal x 4½; **L** detail of glands on outer surface of lateral petal x 24; **M** stamen x 4½; **N** gynoecium x 4½; **P** stigma x 22; **Q** fruit and single twisted valve x 1; **R** seed x 1½. **A**, **B**, **D–K** & **M–R** from *Harley et al.* 26985, **C** from *Lewis & Andrade* 1885, **L** from *Pereira* 9763 & *Pabst* 8652. Drawn by Sue Wickison.

locality, 14 June 1984, *Hatschbach & Kummrow* 47873 (K!, MBM!, NY!); Brumado to Livramento do Brumado, 18 Sept. 1989, *Hatschbach & Nicolack* 53353 (K!); road Brumado to Caetité, 16 June 1986, *Hatschbach & Silva* 50434 (K!); 18 km along rd. from Brumado to Livramento do Brumado, 12 Dec. 1984, *Lewis et al.* CFCR 6720 (K!); 20 km S of Livramento do Brumado, 20 March 1991, *Lewis & Andrade* 1864 (CEPEC!, K!); same locality, 26 March 1991, *Lewis & Andrade* 1885 (CEPEC!, K!, NY!); 10 km S of Livramento do Brumado, 17 April 1991, *Lewis & Andrade* 2000 (CEPEC!, K!); 34 km S of Livramento do Brumado, 12 March 1991, *Lewis et al.* 1858 (CEPEC!, K!); 27 km S of Livramento do Brumado, 22 April 1991, *Lewis & Andrade* 2003 (BR!, CEPEC!, K!, NY!); Rio das Contas, March 1817, *Princeps Maximilianus Neovidensis* s.n. (holotype BR!); 26 km from Anagé on route to Sussuarana, 27 Jan. 1965, *Pereira* 9763 *& Pabst* 8652 (F!, K!, M!, NY!).

ECOLOGY. Caatinga, especially in disturbed areas, 450--500 m.

PHENOLOGY. Flowering from November to June, fruiting from November to June and sometimes into September. Flowering is rain pulsed and shrubs sometimes flower twice in one year.

VERNACULAR NAME. "Pau de galinha".

NOTES. Amongst the Brazilian *Caesalpinia* species, *C. calycina* is quite distinct and is more closely related to *C. fimbriata* from Bolivia and *C. gilliesii* and related taxa from Chile and Argentina than to other Brazilian taxa. With the exception of one collection from Pernambuco, the species is narrowly restricted to the caatinga of south central Bahia. It is pollinated by various *Xylocopa* species. The pollination biology of *C. calycina* is discussed in some detail and compared with that of *C. pluviosa* var. *sanfranciscana* in Appendix 2.

36. **Caesalpinia gilliesii** (*Hook.*) *D. Dietr.*, Synop. Pl. 2: 1495 (1840).

Type: Argentina, near Rio Quatro and Rio Quinto, and near La Punta de San Luis, *Gillies* s.n. (holotype K!).

Poinciana gilliesii Hook., Bot. Misc. 1: 129 (1829).

Erythrostemon gilliesii (Hook.) Link, Klotsch & Otto, Ic. Pl. rar. 1: 97 (1844).

Unarmed shrub to 3 m tall; young stems glabrous. *Leaves* bipinnate; stipules lanceolate-ovate to deltate or suborbicular, 3--4 mm long, pubescent, margins fimbriate-

glandular, subpersistent; petiole 1.5--3 cm long; rhachis 9.5--21.5 cm long; pinnae in 8--15 opposite (proximal) to alternate (distal) pairs plus a terminal pinna; leaflets in 7--11 opposite pairs per pinna, oblong-elliptic to narrowly ovate, ± fleshy, 6--11 x 2--3 mm, both surfaces glabrous, midvein only evident on lower surface, blades with a submarginal row of black punctate glands, these sometimes sparse and occasionally lacking. *Inflorescence* a terminal multi-flowered raceme, the pedicels and rhachis spreading pubescent and densely stipitate-glandular with pixie-cup glands, the calyces less so; bracts lanceolate-ovate, acuminate, 1.8--2.3 cm long, pubescent, the margins fimbriate-glandular, caducous prior to flower anthesis; pedicels 2--3 cm long, not articulated, abscising at base only. *Calyx* lobes 1.8--2.5 cm long, margins fimbriate, stipitate-glandular. *Corolla* yellow, standard broadly obovate, 2.2--3.2 x 1.7--2 cm, lacking a claw and without appendage, eglandular; upper lateral petals broadly obovate, 2.2--3.2 x 1.6--1.8 cm; lower laterals broadly obovate, 2.2--3.2 x 1.2--1.6 cm, the four laterals lacking a claw, glabrous and eglandular. Stamen filaments crimson, 7--9.5(--12) cm long, pubescent on the basal 1--1.5 cm; anthers 3 x 1.5 mm. Ovary densely pubescent and stipitate-glandular, ovules up to 10; style crimson, c 9--10(--12) cm long, pubescent on at least lower $^1/_3$; stigma terminal, funnel-shaped, unfringed. Fruit a subligneous, elastically dehiscent pod, 8--10.8 x 1.9--2.1 cm, valves finely pubescent (the hairs most evident on the suture), glandular with stipitate pixie-cup glands but these wear off as fruit matures, valves twist after dehiscence, up to c 6-seeded. *Seeds* brown, ovate, c 10 x 9 x 2 mm. *Seedling* germination phaneroepigeal, cotyledons foliaceous, apex rounded, base cordate, first eophyll pinnate with 7--8 pairs of opposite to alternate leaflets, second eophyll bipinnate with one pair of opposite pinnae plus a terminal pinna, each with 5--6 pairs of opposite leaflets, stipules with a fimbriate, gland-tipped margin, hypocotyl glabrous, epicotyl pubescent with gland-tipped hairs. (Figs. 3A & **57**, Map 20).

DISTRIBUTION. A native of Argentina, and possibly Uruguay, known from Chile and Peru but probably introduced, widely cultivated elsewhere.

ARGENTINA: Catamarca, Sta. Maria, 22 Nov. 1949, *Barkley* 19 Ar 280 (K!); Prov. of San Juan, San Agustin, 31 Jan. 1943, *Bartlett* 19544 (F!); Prov. Catamarca, El Jumial, 23 Nov. 1950, *Brizuela* 1431 (BR!); E. Rios, Paraná, Paracao, 31 Oct. 1962, *Burkart et al.* 23692 (K!); Prov. La Rioja, Depto. General Lavalle, 25 Jan. 1974, *Cabrera et al.* 24566 (MBM!); Salta, Depto. Guachipas, 9 Nov. 1978, *Cabrera et al.*

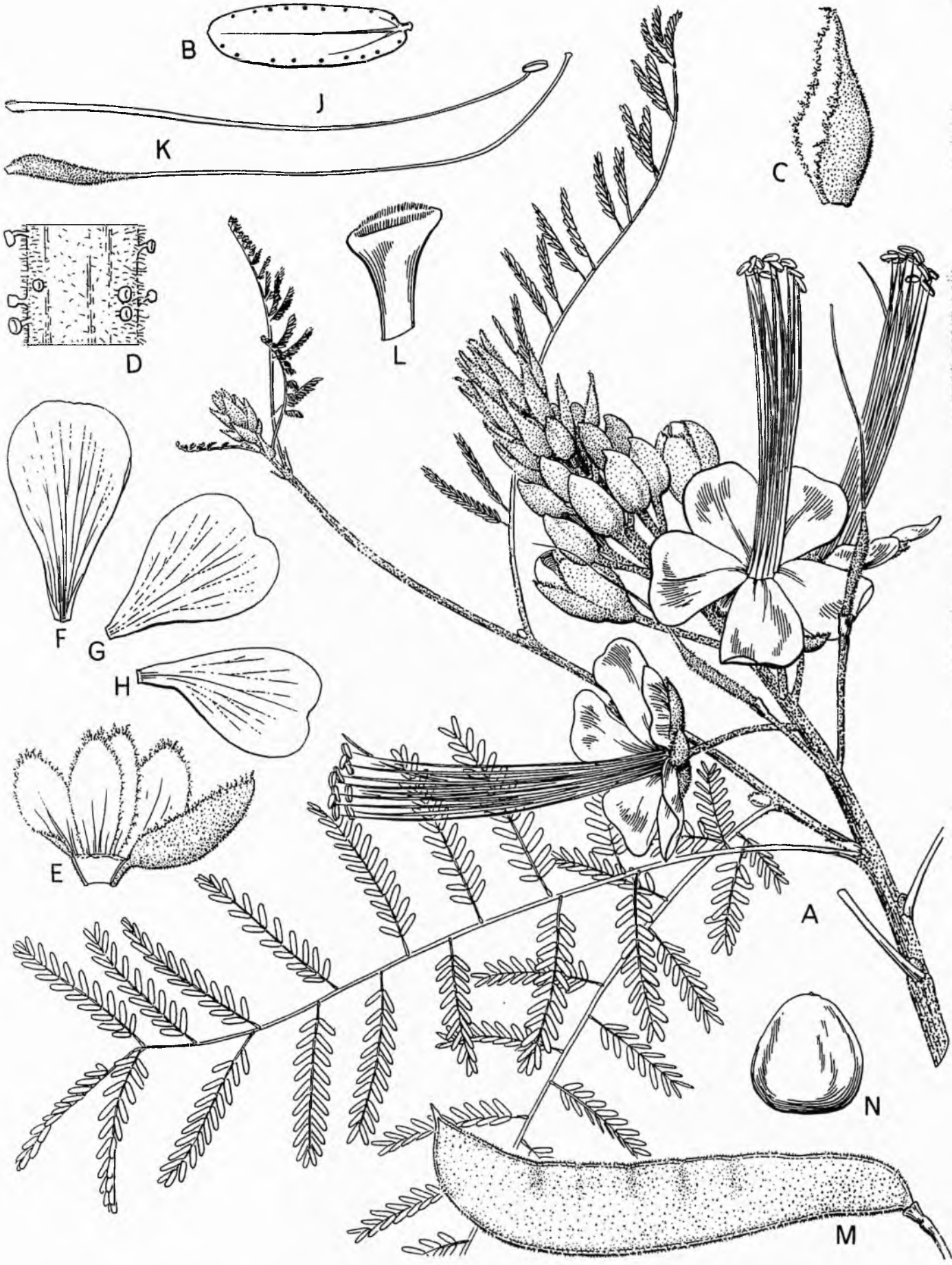
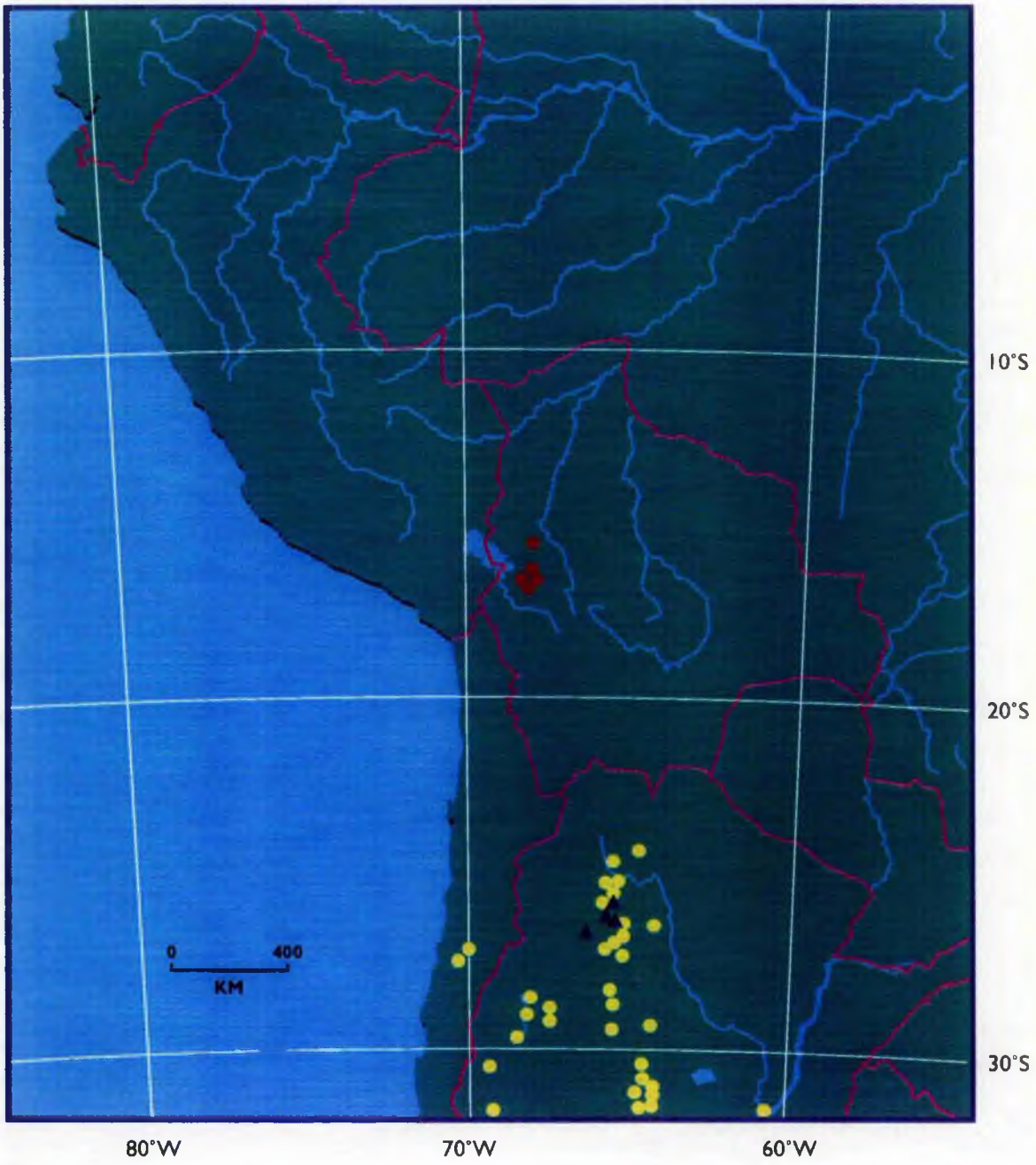


FIG. 57. *Caesalpinia gilliesii*. **A** flowering branch x 1; **B** leaflet undersurface showing submarginal glands x 6; **C** bract x 2¼; **D** glandular pedicel x 15; **E** calyx opened out x 1½; **F** standard petal x 1½; **G** upper lateral petal x 1½; **H** lower lateral petal x 1½; **J** stamen x 1½; **K** gynoecium x 1½; **L** stigma x 22½; **M** fruit x 1; **N** seed x 3. **A** from *Venturi* 5365, **B** & **M** from *Kiesling et al.* 4891, **N** from *Lewis* 1417, the rest from Cult. Kew 213-69.01878 (source Palermo Bot. Gard., Sicily). Drawn by Eleanor Catherine.

Distribution of *Caesalpinia exilifolia* (▲) *C. fimbriata* (●) and *C. gilliesii* (○) in western South America



29721 (F!, K!); Prov. Córdoba, Depto. Isehilin, 2 Nov. 1945 *Cuezzo* 724 (F!, K!); San Juan, Iglesia, El Rodeo, 13 Dec. 1945, *Cuezzo* 1874 (K!); vicinity of General Roca, Sept. 1914--Feb. 1915, *Fischer* 184 (F!, K!); Buenos Aires, without date, *Fox* 250 (K!); near Rio Quatro, without date, *Gillies* s.n. (holotype K!); Prov. Córdoba, Sierra Grande, 16 Dec. 1938, *Goodspeed* 17238 (K!); Córdoba, Dec. 1874, *Grisebach* 81 (K!); Monte, Feb. 1912, *Hauman* L36 (BR!); nr. Córdoba, 12 Nov. 1877, *Hieronymus* 20 (BR!, F!, HBG!, K!); Córdoba, Oct. 1879, *Hieronymus* s.n. (BR!); San Juan & San Luis, 1871--72, *Jameson* s.n. (K!); Tucumán, Oct. 1930, *Kanter* 60 (HBG!); Catamarca, Feb. 1931, *Kanter* 54 (HBG!); Prov. Catamarca, Depto. Belen, 23 Dec. 1972, *Kiesling* 157 (MBM!); Prov. Tucumán, Depto. Trancas, 6 km S of Vipos, 6 Jan. 1969, *Krapovickas & Cristóbal* 14546 (MBM!); Prov. Salta, Depto. San Carlos, 4 Jan. 1972, *Krapovickas & Cristóbal* 20628 (MBM!); Tucumán, Oct. 1892, *Kuntze* s.n. (F!); Córdoba, June-Dec. 1874, *Lorentz* 31 (BR!); Prov. Córboda, Feb. 1925, *Lossen* 165 (F!); Prov. Salta, Depto. Anta, Chañarmuzo, 28 Jan. 1948, *Luna* 682 (BR!); Prov. La Rioja, Depto. Chilicito, 10 Jan. 1942, *Meyer* 3502 (F!); Prov. Salta, Depto. La Viña, Coronel Moldes, 31 Jan. 1941, *Meyer* 3888 (F!); Córboda, Villa García, 11 Jan. 1940, *Meyer* s.n. (F!); Prov. La Rioja, Guandacal, 3 Feb. 1942, *Meyer* 4206 (F!); Prov. La Rioja, Villa Castelli, 20 Jan. 1942, *Meyer* 4059 (F!); Prov. La Rioja, Depto. Famatina, 6 Feb. 1942, *Meyer* 4234 (F!); Prov. La Rioja, Vinchina, 17 Jan. 1942, *Meyer* 4033 (F!); Prov. Córdoba, Depto. Colón, La Granja, 14 March 1944, *O'Donell & Rodrigues* 453 (F!); Tucumán, Tafi Viejo, 7 Nov. 1978, *Renvoize et al.* 3379 (K!); Prov. Catamarca, Depto. Paclin, La Merced, 24 Dec. 1946, *Risso* 231 (BR!); Tucumán, Depto. Trancas, 19 Nov. 1974, *Ruiz et al.* 10614 (F!); Mendoza, Las Heras, 10 Dec. 1944, *Semper* 192 (NY!); Prov. Córdoba, Depto. Punilla, Cerro Uritorco, 3 Jan. 1951, *Sota* 3520 (BR!); Prov. Córdoba, Depto. Punilla, Los Cocos, 17 Dec. 1950, *Sota* 3275 (BR!); Tucumán, Tafi, 19 Nov. 1946, *Sparre* 762 (K!); Catamarca, Valle Viejo, 1915, *Tellechea* 72 (BR!); Prov. Santiago del Estero, Depto. Ojo de Agua, 22 Dec. 1981, *Ulibarri* 1340 (K!); Prov. Tucumán, Depto. Leales, Campo Azul, 10 Nov. 1946, *Vaca* 40 (BR!); Prov. Catamarca, Depto. del Alto, Balevzua, 18 Jan. 1928, *Venturi* 7168 (F!); Prov. Jujuy, Depto. San Pedro, Santa Clara, 19 Oct. 1929, *Venturi* 9727 (K!); Tucumán, Depto. Capital, 6 Oct. 1927, *Venturi* 5365 (F!, K!); Prov. Córboda, Depto. Punilla, Los Cocos, 24 Jan. 1947, *Villafañe* 519 (BR!); Prov. Córdoba, Depto. Punilla, La Cumbre, 25 Jan. 1947, *Villafañe* 542 (BR!): **URUGUAY**, Montevideo, 17 June 1874, *Fruchard* s.n. (F!); Montevidio, March 1858, *Gilbert* 113 (K!); **PERU**, Arica, 2 May 1882, *Ball* s.n. (K!); Prov. Chancay, Depto. Lima, km 79 road Huacho to Churin, 17 Dec. 1964, *Saunders* 1002 (K!); **CHILE**, Tierra Amarilla, 13 km SSE of Copiapo, 7 Nov. 1989, *Aronson* 7726 (K!); Prov. Atacama, Caldera, 21 Feb. 1939, *Beetle* 26130 (K!).

CULTIVATED in Spain, Greece, Cyprus, Sicily, Israel, Turkey, Egypt, Afghanistan, Iran, Iraq, Canary Islands, USA, Mexico, Puerto Rico, Libya, Eritrea, Ethiopia, Kenya, Tanzania, Zimbabwe, Mozambique and SW Africa.

ECOLOGY. Rocky thorn scrub forest, (5--)250--1620 m (within native range).

PHENOLOGY. Known to flower and fruit almost all year in Argentina (but no records for April other than for cultivated material in the USA and Kenya).

VERNACULAR NAMES. "Mal de ojos", "Lagaña de perro", "Mal de Perro", "Disciplina de monja", "Barba de Chivo", "Piscala".

37. **Caesalpinia fimbriata** *Tul.* in Arch. Mus. Hist. Nat. Paris 4: 145 (1844). Type: Bolivia: "Chivesivi, Vallé S de La Paz, alt. 8500-12000 ped. angl.", *Pentland* 39 (holotype P!, isotype F!).

Caesalpinia bangii Rusby in Mem. Torrey Bot. Club 3(3): 22 (1893). Type: Bolivia, 1891, *Bang* 757 (holotype NY!, isotypes E!, F!, GH!, K!).

Caesalpinia cromantha Burkart in Rev. Argent. Agron. 3(2): 100 (1936). Type: Argentina, Prov. Salta, Depto. Guachipas, Pampa Grande, Jan. 1897, *Spegazzini* 2198 (holotype SI, isotype LP).

Unarmed shrub, to c 2 m tall; stems densely pubescent with plumose-stipitate glands intermixed, with age glabrescent. *Leaves* bipinnate, stipules ovate-lanceolate to ovate-suborbicular, c 6 mm long, outer face and fimbriate margin pubescent, fimbriae gland-tipped; petiole 1.2--4 cm long; rhachis 2.5--6 cm long, short-pubescent; pinnae in 2--6(--7) opposite pairs plus a terminal pinna; leaflets in 6--9(--10) opposite pairs, petiolulate, oblong-elliptic to obovate-elliptic, terminal leaflets 6.5--12 x 3--7 mm, medians 6--16 x 3--7 mm, both surfaces of all leaflets glabrous; venation obscure (leaflets ± fleshy), only the main vein visible on lower surface, margin crenulate, black glands sunken in shallow concave indentations; short-stalked glands sparse on rhachis of pinnae just below leaflet petiolules. *Inflorescence* an axillary or teminal, c 30--75-flowered sessile or shortly-pedunculate raceme, densely pubescent with short, white, patent hairs, short-stalked pixie-cup glands intermixed; bracts ovate, acuminate, 10--12(--20) mm long, pubescent, glandular, fimbriate, caducous; pedicels 3--6 mm long, pubescent, glandular, articulated c 1--1.5 mm below calyx (but zone of articulation sometimes not clear). *Calyx* lobes 8--12 mm long, pubescent, sessile and stipitate pixie-cup glands intermixed with pubescence, lower lobe imbricate-cucullate, fimbriate. *Corolla* yellow; standard petal darker yellow speckled orangish-red on inner surface, blade suborbicular to elliptic, apex rounded, 11.5--

14 x 8.5--10.5 mm (including a 1.5--2 mm claw), claw and lower $^{1}/_{2}$--$^{2}/_{3}$ blade thickened, a small tuft of hairs on claw margins; upper petals oblanceolate to obovate, 14--17 x 7--10 mm (including a 1 mm sparsely pubescent claw); lower laterals obovate to broadly oblanceolate, 14--17 x 5.5--8.5 mm (including a 1 mm claw). Stamen filaments 10--11 mm long, densely pubescent on lower $^{1}/_{2}$--$^{2}/_{3}$, those on either side of the vexillary one each have much more pubescent bases than all others; anthers 2.75 x 1--1.25 mm. Ovary densely pubescent and glandular (with the glands usually densest nearer to upper margin); style c 7.5--8 mm long (much shorter on rudimentary pistils of essentially male flowers); stigma a terminal, fringed, tubular or slightly flared chamber. *Pod* chartaceous to subcoriaceous, elastically dehiscent, 4--5.7 x 1.2--1.7 cm (including a 2 mm beak), valves twist after dehiscence, moderately to densely pubescent, especially on the margins, scattered stipitate pixie-cup glands intermixed (with age these rubbing off to leave slightly raised dots), (2--)3--5-seeded. *Seeds* dark brown, dull and unmottled to brown speckled reddish-brown and shiny, ovate to suborbicular, 7--7.5 x 4.5--6 x 1.25--1.5 mm. (Fig. 58, Map 20.)

DISTRIBUTION. Bolivia and Argentina.

BOLIVIA: without locality, 1891, *Bang* 757 (holotype NY!, isotypes E!, F!, GH!, K!); Depto. La Paz, Prov. Murillo, La Paz-Calacoto, 16 Nov. 1980, *Beck* 4029 (NY!); La Paz, Nov. 1911, *Buchtien* 3180 (NY!); Huaricana, 5 Aug. 1906, *Buchtein* 107 (NY!); Depto. La Paz, Prov. Murillo, 12 Dec. 1979, *Feuerer* 7136a (K!); Valle abajo, 11 Nov. 1973, *Graf* 245 (NY!); Rio abajo, 30 Sept. 1973, *Graf* 187 (NY!); without exact locality, without date, *Pentland* 39 (holotype P!, isotype F! [fragment], K! [photo]); Depto. La Paz, Prov. Murillo, 18 km SE of La Paz, 20 Sept. 1986, *Solomon* 15619 (NY!); 2 km SE of Mecapaca, 24 Feb 1980, *Solomon* 5076 (K!); c 13 km SE of Calacoto, 30 Jan. 1983, *Solomon* 9448 (K!); 18 km SE of La Paz, 4 June 1985, *Solomon* 13819 (K!); same locality, 8 Feb. 1984, *Solomon & Kuijt* 11490 (K!); 14 Feb. 1987, *Solomon & Nee* 16062 (K!); Bellavista, 9 Nov. 1926, *Troll* 2827 (M!); *Troll* 2826 (M!); **ARGENTINA**, Prov. Jujuy, Depto. Santa Barbosa, La Quinta, 1 Nov. 1970, *Cabrera* 20837 (E!); Catamarca, El Rodeo, Jan. 1910, *Castillón* s.n. (A!).

ECOLOGY. Semi-arid thorn scrub; open, spiny cactus scrub; disturbed, low thorny woodland, 1300--3200 m.

PHENOLOGY. Flowering from August to February, fruiting from November to February (with one record for June).

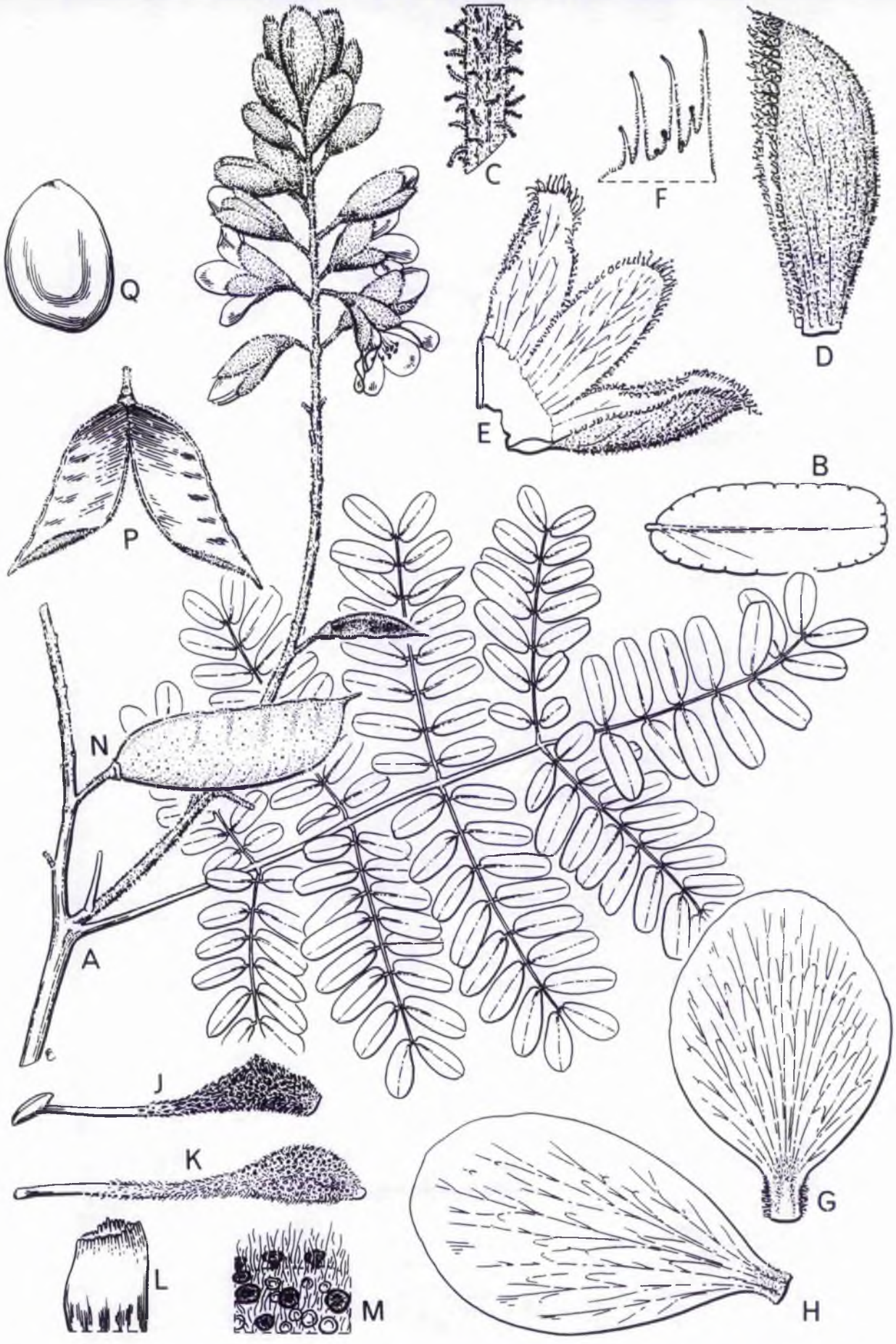


FIG. 58. *Caesalpinia fimbriata*. **A** inflorescence and bipinnate leaf x 1; **B** median leaflet undersurface x 3; **C** stem glands x 7½; **D** bract x 3; **E** ½ calyx opened out x 3; **F** calyx lobe detail x 7½; **G** standard petal x 4½; **H** upper lateral petal x 4½; **J** stamen x 4½; **K** gynoecium x 4½; **L** stigma x 30; **M** detail of ovary glands x 30; **N** fruit x 1; **P** dehisced fruit x 1; **Q** seed x 4½. **A–M** from *Solomon & Kuijt* 11490, **N** from *Solomon & Nee* 16062, **P & Q** from *Solomon* 13819. Drawn by Eleanor Catherine.

38. **Caesalpinia mimosifolia** *Griseb.*, Pl. Lorentz: 80 (1874). Type: Argentina, Catamarca, Cuesta de Chilca, *Lorentz* 515 (holotype GOET!, isotype CORD, n.v.).

Unarmed shrub, 0.5--1.5 m; young stems red, glabrous, densely glandular with short-stipitate sticky glands, occasionally some parts finely puberulous, older stems glabrous and eglandular. *Leaves* bipinnate; stipules ± foliaceous, ovate to obovate, apex rounded to acute, 2.5--4 x 1.5--2.5 mm, stipitate-glandular, caducous; petiole (0.8--)2.5--3.7 cm long, stipitate-glandular; rhachis (0.9--)2--5 cm long, short-stalked glandular, slightly articulated at pinnae insertions; pinnae in 3--5 opposite pairs plus a terminal pinna; leaflets in 6--12 opposite pairs per pinna, oblong-obovate to oblong-elliptic, slightly falcate, obtuse, the basal ones on each pinna deeply crenulate, the terminal leaflets 2.5--4.5 x 1--2 mm, median ones 3--8 x 1.25--2 mm, both surfaces glabrous; venation obscure, only the main vein visible on the lower surface (flush with leaflet surface), excentric, dividing the blade 2: 1 or 1.5: 1; leaflet margin variable, usually crenate with red glands in deep sulcate depressions (especially on proximal leaflets of each pinna), sometimes only glandular on one side or glands lacking and leaflet margin entire (especially on distal leaflets of pinnae). *Inflorescence* a terminal or leaf-opposed, 5--21 cm long, c 8--25-flowered raceme, rhachis glabrous or obscurely puberulous, eglandular distally, stipitate-glandular proximally, sometimes densely so; bracts ovate or ovate-lanceolate, apiculate, 2.75--4 mm long, finely pubescent, stipitate-glandular, margin fimbriate; pedicels (7--)9--12(--15) mm long, finely pubescent or glabrous, stipitate-glandular, especially below calyx, articulated 1--1.5 mm below calyx. *Calyx* lobes 7--9 mm long, sparsely to densely puberulous, sparsely glandular, the lower lobe ± cucullate, obscurely fimbriate at apex. *Corolla* yellow or orangish; standard petal blade obovate, 10.5--11.5 x 4.5 mm, basal $^1/_2$ inrolled, claw pubescent; upper lateral petals obovate, 11 x 5--8.5 mm, lower laterals obovate, 11 x 4.5--6.5 mm, laterals with claw sparsely pubescent. Stamen filaments red, spreading pubescent on basal $^1/_3$--$^2/_3$, sometimes very sparsely so on upper $^1/_3$; anthers 0.75--1.5 x 0.5 mm. Ovary glabrous or almost so, densely glandular with sessile and/or short-stipitate glands; style c 9 mm long, basal $^1/_2$ with short-stipitate glands; stigma a terminal, fringed chamber, somewhat curved upwards. *Pod* coarsely chartaceous,

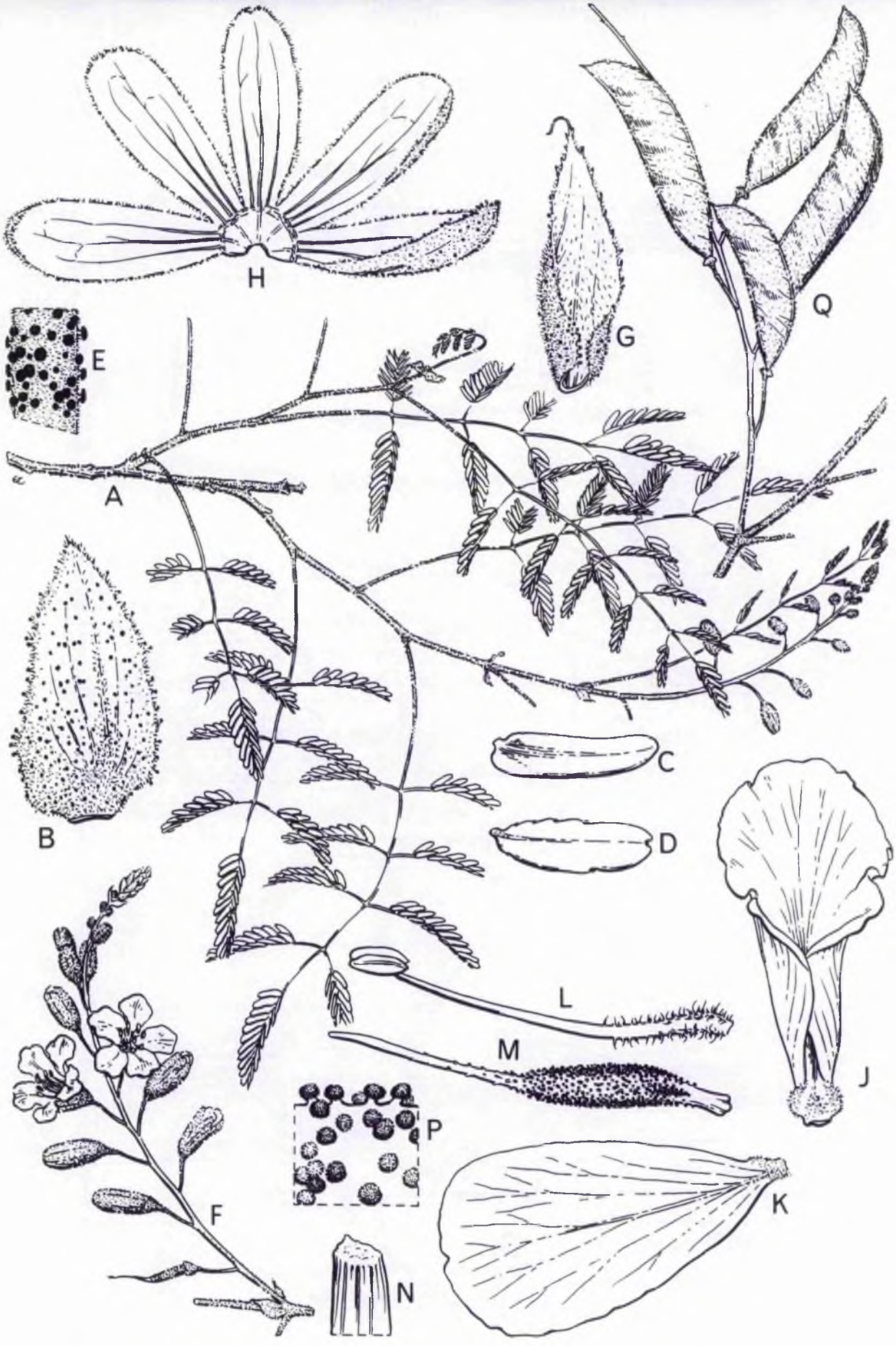
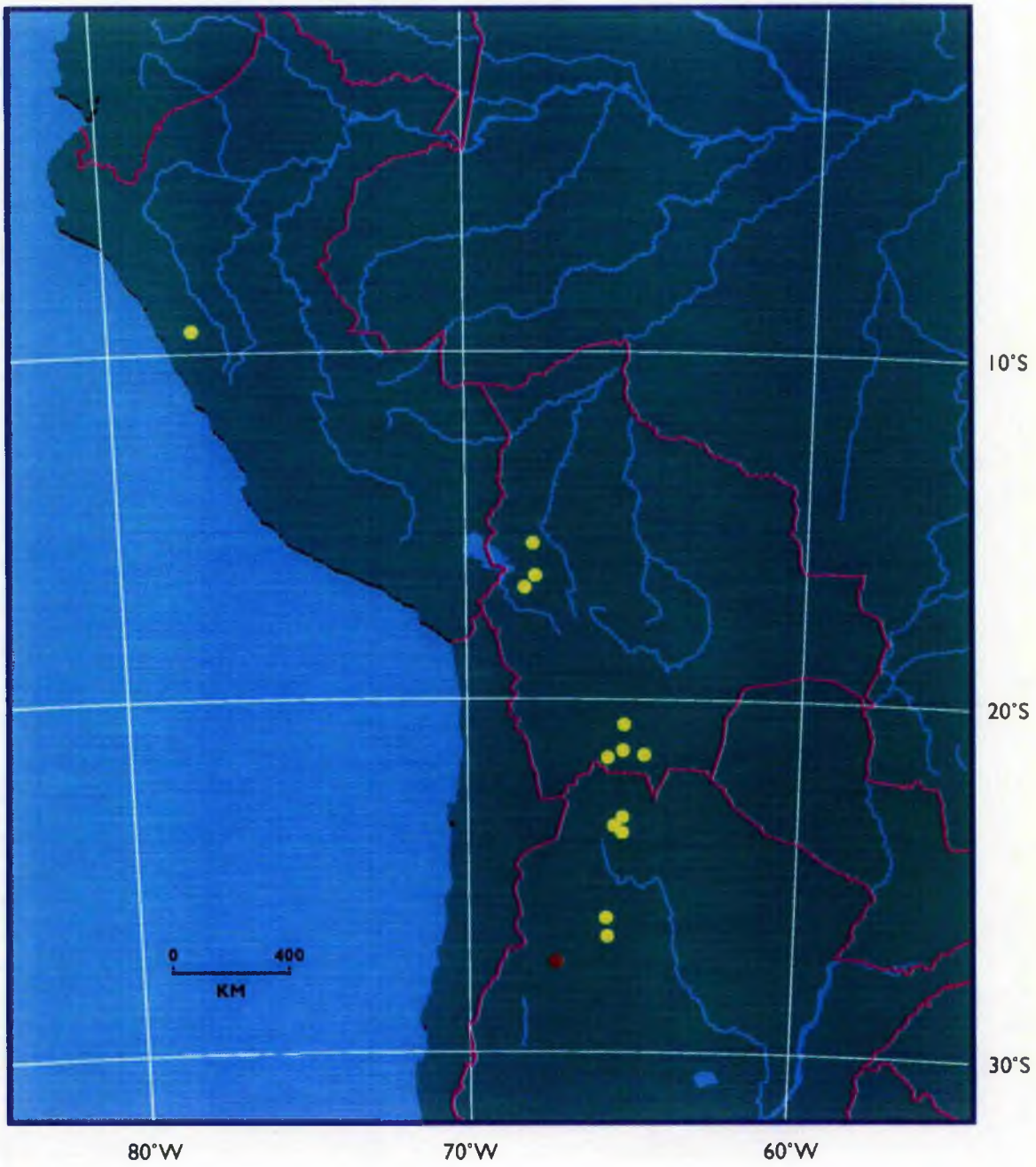


FIG. 59. *Caesalpinia mimosifolia*. **A** flowering branchlet x 1; **B** stipule x 12; **C** eglandular leaflet undersurface x 6; **D** glandular leaflet undersurface x 6; **E** glands on stem x 15; **F** inflorescence x 1; **G** bract x 12; **H** calyx opened out x 4½; **J** standard petal x 6; **K** lateral petal x 6; **L** stamen x 6; **M** gynoecium x 6; **N** stigma x 48; **P** glands on ovary x 48; **Q** fruits x 1. **F** from *Lorentz* s.n., **Q** from *Schreiter* 68526, the rest from *Kiesling et al.* 4990. Drawn by Eleanor Catherine.

Distribution of *Caesalpinia mimosifolia* (●) (range greater than shown - most collections with data inadequate for mapping) and *C. trichocarpa* (○) in western South America



elastically dehiscent from apex, falcate in upper half, 3--4.7 x 0.7--0.9 cm, glabrous, a few scattered glands near base but these rub off with age, 3--5(--6)-seeded. *Seeds* obliquely ovate, 5 x 4.5 x 0.75 mm, dark brown or orange mottled dark brown, shiny. (Fig. **59**, Map 21).

DISTRIBUTION. NW Argentina, and southern Bolivia (according to the literature, but Bolivian material probably referrable to *C. trichocarpa*). In Argentina recorded from the west of the mountainous zone from the Sierras of San Luis and Córdoba, through those of La Rioja, Catamarca and Tucamán to Salta and Jujuy.

ARGENTINA: Prov. San Luis, 6 Nov. 1940, *Burkart* 10718 (K!); Prov. of Córdoba, Cruz del Eje, 11 March 1877, *Hieronymus* 684 (photo, F!); San Juan, Depto. Valle Fértil, Los Bretes, 28 Nov. 1984, *Kiesling et al.* 4990 (NY!); Catamarca, without date, *Lorentz* s.n. (K!); Prov. Córdoba, Feb. 1925, *Lossen* 164 (F!, M!); Prov. Catamarca, Fuerte de Andalgalá, Jan. 1876, *Schickendantz* 156 (K!); Catamarca, Depto. Belén, La Puerta de San José to La Estancia, March 1939, *Schreiter* 68526 (F!).

ECOLOGY. Little information available, 1200--1500 m.

PHENOLOGY. Flowering from November to March, fruiting January to March.

VERNACULAR NAME. "Pishcalilla" given in Burkart (1936), fide Spegazzini.

NOTES. Closely related to *C. trichocarpa* which has shorter leaf rhachides, fewer leaflets per pinna and plumose gland-tipped trichomes on the shorter fruits.

The holotype of *C. mimosifolia* is *Lorentz* 515 from Cuesta de Chilca at Goettingen. The field label on this specimen mentions various localities where the species is known to grow in addition to the actual collection site. Fuerte de Andalgalá and Belén, two of the three localities given by Grisebach in the protologue of *C. mimosifolia*, are both (the first abbreviated to 'Fuerte') mentioned on this same field label and it thus seems conclusive that the geographical citation in the protologue refers to one collection and not to three syntypes. Burkart (1936) studied a duplicate of *Lorentz* 515 at Córdoba and also gave the collection locality as Cuesta de Chilca but went on to say that this is 'a duplicate of the third example cited by Grisebach in the original description', erroneously presuming them to be syntypes.

39. **Caesalpinia trichocarpa** *Griseb.* in Symb. Flor. Argent.: 112 (1879). Type: Argentina, Jujuy, San José de Tilcara, May 1873, *Lorentz & Hieronymus* 848 (fide Burkart in Rev. Argent. Agron. 3(2): 92 (1936)) (holotype GOET!, isotypes CORD, SI, photo F!).

Caesalpinia fisheriana Rusby in Mem. Torrey Bot. Club 3(3): 23 (1893). Type: Bolivia, 1891, *Bang* 756 ("in part, perhaps distributed as 756a") (holotype NY!, isotypes E!, F!, GH!, K!).

Caesalpinia rosulata Rusby, loc. cit. 3(3): 23 (1893). Type: Bolivia, 1891, *Bang* 756 (in part) (holotype NY!, isotypes F!, GH!, K!).

Unarmed, glandular shrub, 0.3--1.5 m; peduncles, pedicels, petioles, leaf rhachides, calyces and leaflet margins usually densely glandular; young stems sparsely puberulous, glabrescent, glandular, older stems glabrous. *Leaves* bipinnate; stipules ovate, 2--3 x 2 mm, margin fimbriate; petiole 0.4--2.8 cm long; rhachis 0.5--2.8 cm long; pinnae in (1--)2--4(--5) opposite pairs plus a terminal pinna; leaflets in (4--)5--7(--8) opposite pairs, elliptic to oblong-obovate, 2.5--7 x 1.25--3.5 mm, apex obtuse to rounded, upper surface glabrous or almost so, lower surface puberulous, especially on the margins, to glabrous; venation obscure, the main vein ± visible on lower surface, the margin (especially of proximal leaflets of each pinna) crenulate with sunken glands in the concave indentations, sometimes lower surface of blade also glandular with dark, sessile glands. *Inflorescence* a terminal or leaf-opposed, erect or somewhat deflexed, 3--6 cm long, 5--18(--28)-laxly flowered raceme, the rhachis very finely puberulous; bracts ovate to ovate-lanceolate, concave, 2--4.5(--9) mm long, pubescent, glandular; pedicels 4.5--13 mm long, pubescent, rarely eglandular, articulated 0.5--1.5 mm below calyx. *Calyx* red, pubescent, rarely eglandular, the lobes 5--8 mm long, lower lobe imbricate-cucullate. *Corolla* yellow to orangish; dorsal face of standard petal reddish, blade oblong-rectangular to subrhomboid, obtuse, 8--11.5 x 3.5--5 mm, the small claw pubescent; upper lateral petals obovate, 8.5--10.5 x 4--6 mm; lower laterals obovate, 8.5--10 x 4--5.5 mm, the claws of lateral petals glabrous, or almost so. Stamen filaments red, 7.5--9 mm long, spreading pubescent on basal $^1/_2$; anthers 1.25--1.5 x 0.5--1 mm. Ovary with a dense indumentum of plumose, gland-tipped trichomes; style c 5 mm long, stipitate-glandular on basal $^1/_4$, widening slightly towards apex; stigma a terminal, obscurely fringed, chamber. *Pod* lunate-falcate,

FIG. 60. *Caesalpinia trichocarpa*. **A** flowering and fruiting branchlet x 1; **B** bract x 9; **C** median leaflet undersurface x 12; **D** median leaflet undersurface (showing variation) x 12; **E** calyx opened out x 4½; **F** detail of calyx lobe margin x 24; **G** standard petal x 4½; **H** lateral petal x 4½; **J** stamen x 9; **K** gynoecium x 9; **L** stigma x 60; **M** detail of ovary trichomes x 60; **N** fruits x 1; **P** detail of fruit trichomes x 24; **Q** seed x 6. **B**, **D** and **N–Q** from *Burkart* 5358, the rest from *Balls* B6058. Drawn by Eleanor Catherine.

apex acute, chartaceous, elastically dehiscent, 2--3 x 0.8--1 cm, moderately to densely covered in 1.5--2 mm long plumose trichomes, (1--)3--4-seeded. *Seeds* dark brown, ovate-orbicular to pyriform, laterally compressed, c 5--6 x 4--5 x 1 mm. (Figs. 5T & **60**, Map 21).

DISTRIBUTION. Peru, Bolivia and Argentina (Jujuy, Salta, Tucumán and Catamarca).

PERU: without exact locality or date, *Haenke* s.n. (M!); Dept. Ancash, Callejón de Huaylas, 9 April 1970, *Smith & Blas* 4891 (F!, SI); **BOLIVIA**, 1891, *Bang* 756 (E!, F!, GH!, K!, NY!); Dept. La Paz, Prov. Murillo, 12 March 1981, *Feuerer* 5446c (HBG!); Depto. La Paz, 4 March 1982, *Feuerer & Menhofer* 10140a (K!); Camargo, nr. Tarija, 13 Feb. 1904, *Fiebrig* 2981 (K!); Condor, nr. Tarija, 6 Feb. 1904, *Fiebrig* 2983 (E!); *Fiebrig* 2983a (M!); Rencillo, nr. Tupiza, 28 Feb. 1904, *Fiebrig* 3112 (E!, K!); *Fiebrig* 3112a (M!); Depto. La Paz, Prov. Murillo, Hacienda Huajchilla, 18 km SE of La Paz, 14 Feb. 1987, *Solomon & Nee* 16058 (K!); Depto. Chuquisaca, Prov. Sud Cinti, c 2 km before Impora on road from Tupiza to Las Carreras, 5 Dec. 1967, *Vuilleumier* 409 (NY!, TEX!); **ARGENTINA**, Jujuy, Alfarsita, nr. Tilcara, 9 Feb. 1939, *Balls* B6058 (E!, F!, K!); Prov. Jujuy, Humahuaca, 29 Feb. 1940, *Burkart & Troncoso* 11935 (K!); Prov. Tucumán, Depto. Tafi, valle de Amaicha, 3 Feb. 1933, *Burkart* 5358 (GH!, K!); Prov. Jujuy, Depto. Tilcara, Maimará, 8 Jan. 1971, *Krapovickas & Cristóbal* 17592 (LL!, MBM!); San José de Tilcara, 1873, *Lorentz & Hieronymus* 848 (photo. of type F!); Prov. Jujuy, Depto. Tilcara, 9 Feb. 1927, *Venturi* 4881 (F!, GH!, NY!); Prov. Salta, Depto. Cafayate, Yacochuya, 4 April 1969, *Vervoorst* 7500 (LL!).

ECOLOGY. Dry, rocky or sandy open slopes in semi-arid spiny cactus scrub, 1500--3100 m.

PHENOLOGY. Flowering from December to May, fruiting from January to May.

VERNACULAR NAME. "Arquita" (fide Ulibarri, 1987).

NOTES. Balls (B6058) recorded the species as a spiny shrub but his remark probably referred to the erect plumose trichomes on many parts of the plant because the species apparently lacks any form of armature.

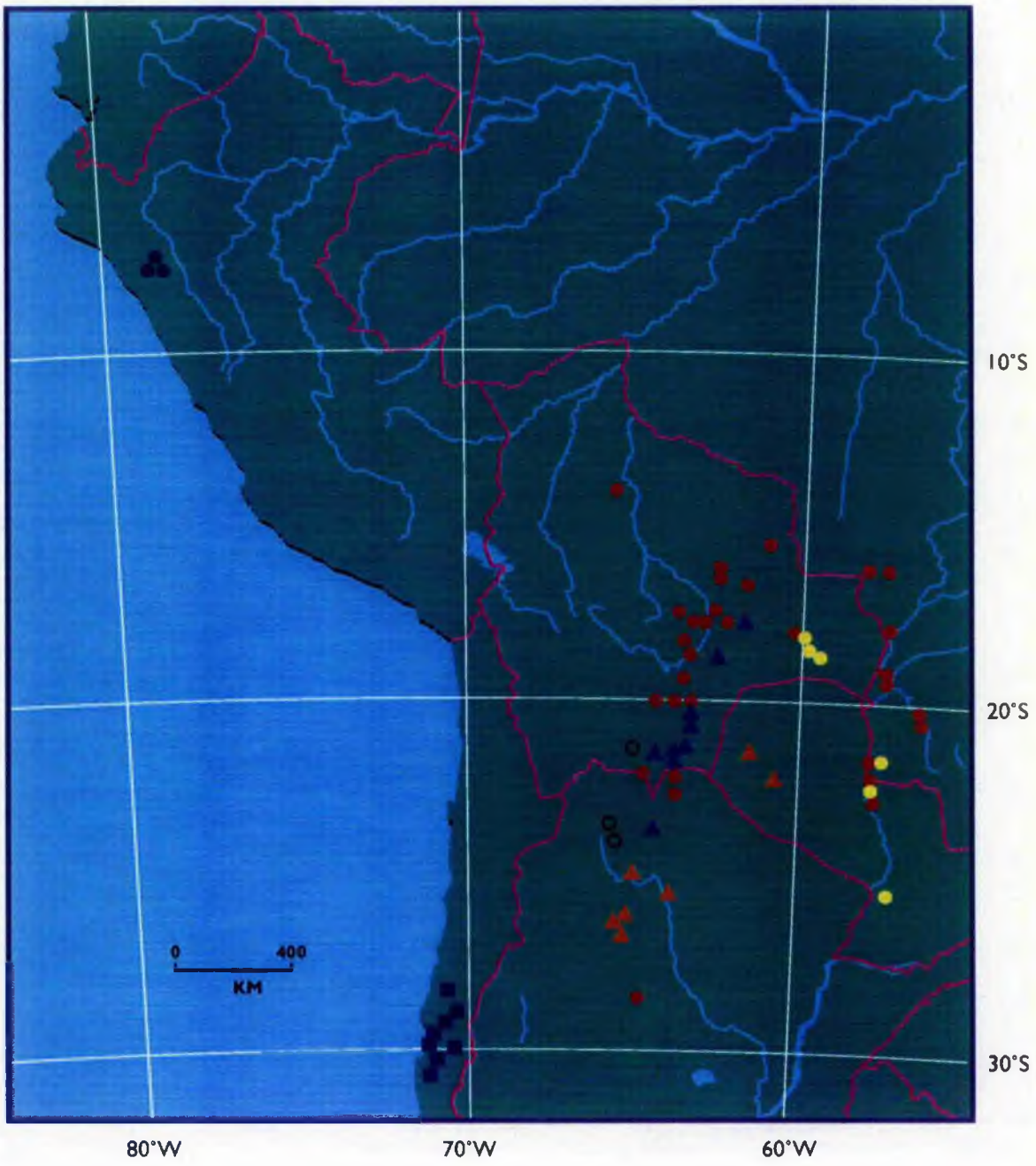
The species is closely related to *C. mimosifolia* but the flowers are generally smaller, the leaves are shorter with few pairs of pinnae and leaflets, and the fruit is shorter and covered in plumose hairs. As with *C. mimosifolia* the leaflets decrease in size towards the distal end of each pinna.

40. **Caesalpinia ancashiana** *Ulibarri* in Darwiniana 30 (1--4): 231 (1991).

Type: PERU, Depto. Ancash, Prov. Recuay, Distr. de Marca (Jarrer Jamanán), 9 Aug. 1963, *Gómez* 94 (holotype USM, n.v.).

Unarmed herb to c 30 cm tall, young stems with shiny white or yellowish orange bark, glabrous. *Leaves* bipinnate; stipules ovate-deltoid, foliaceous, 4.5--5.5 mm long, scarious, subpersistent; petiole 1.2--6 cm long, glabrous, very sparsely glandular, grooved along the upper edge; rhachis lacking, leaf reduced to one opposite pair of pinnae plus a terminal pinna, a corona of gland-tipped, lanceolate-triangular appendages encircling the insertion of the three pinnae; leaflets in (4--)8--10(--11) opposite pairs, oblong to elliptic-obovate, apex rounded to shallowly emarginate, base asymmetric, terminal leaflets 4--10 x 2--4 mm, medians 7--14 x 2.5--4.5 mm, both surfaces glabrous, main vein prominent below, secondaries brochidodromous, obscure, most leaflets eglandular but a few of the proximal ones on each pinna of some leaves with a few sessile, discoid glands near the leaflet base, especially near the margin, occasionally over the blade surface, leaflet margin sometimes obscurely, shallowly crenulate; tiny gland-tipped stipel-like appendages at the base of each leaflet pulvinule. *Inflorescence* a 10--20-flowered terminal or axillary raceme, the rhachis, pedicels and calyces very finely puberulous (glabrous to the naked eye); bracts ovate-lanceolate, acute, c 3 mm long, persistent; pedicels (5--)8--10(--15) mm long, articulated c 2 mm below calyx. *Calyx* lobes c 7 mm long, finely tomentulose on inner surface. *Corolla* orangish-yellow; standard petal blade ovate, 10 x 6 mm (including a 2 mm claw), dorsal surface of blade densely stipitate-glandular with pixie-cup glands, claw lacking an appendage, a few hairs on the margin basally; upper lateral petals elliptic, c 8.5 x 5.5 mm (including a 0.75 mm claw), blade eglandular, claw sparsely pubescent and sparsely glandular on margins; lower laterals narrowly oblong-elliptic, 9 x 4 mm (including a 0.75 mm claw), blade eglandular, claw very sparsely pubescent, eglandular. Stamen filaments 7.5--9 mm long, basal $^{1}/_{3}$--$^{1}/_{2}$ with transparent hairs, basal $^{2}/_{3}$--$^{3}/_{4}$ with stipitate, club-shaped glands. Ovary sparsely pubescent along upper margin, stipitate, club-shaped glands moderately dense over most of the surface, especially on the suture; style sparsely to moderately glandular; stigma a terminal fringed chamber. *Fruit* a thinly woody, dehiscent pod, 3.5 x 1.05 cm, sparsely puberulous, glabrescent, sparsely glandular with

Distribution of *Caesalpinia ancashiana* (●) *C. angulata* (■) *C. argentina* (▲) *C. coluteifolia* (▲) *C. coulterioides* (○) *C. marginata* (○) and *C. pluviosa* var. *pluviosa* (●) in western South America



short-stalked glands, the hairs and glands most evident on the suture, ?1--3-seeded. (Map 22)

DISTRIBUTION. Endemic to Peru.

PERU: Depto. Ancash, prov. Recuay, Distr. de Marca (Jarrer Jamanán), 9 Aug. 1963, *Gómez* 94 (holotype USM); Depto. Ancash, Prov. Recuay, road Pativilca-Conococha, 27 May 1970, *López et al.* 7614 (SI); Depto. Cajamarca, between Lives and Payae, 11 May 1977, *Sagástegui et al.* 8785 (F!, MO!, NY!, US!); Depto. Cajamarca, Prov. Contumazá, Andaloy (San Benito - Yetón), 28 March 1985, *Sagástegui et al.* 12544 (K!, NY!); Depto. Cajamarca, Prov. Cajamarca, Qda. del Río San Juan, 20 Jan. 1973, *Sánchez Vega* 990 (SI).

ECOLOGY. On slopes, 1700-2650 m.

PHENOLOGY. Flowering from January to May and also in August, fruiting from March to May.

NOTES. Closely related to *C. mimosifolia* and *C. trichocarpa* but with fewer pinnae per leaf, the stems essentially eglandular and the standard petal densely stipitate-glandular on its dorsal surface. In addition *C. trichocarpa* has plumose trichomes on its developing ovaries and fruits, a character that easily distinguishes it from *C. ancashiana* even when the occasional specimen of the former has leaves reduced to three pinnae. Ulibarri (1991) compares his new species to *C. bangii* (here recognised as a synonym of *C. fimbriata*) and comments that the latter differs from his species by its larger number of pinnae per leaf, smaller leaflets with dark sessile glands on the margin and larger flowers. *C. fimbriata*, as circumscribed in this work, can, however, have larger leaflets than those of *C. ancashiana* and based on two collections (namely *Sagástegui et al.* 8785 and *Sagástegui et al.* 12544) both named by Ulibarri as *C. ancashiana* after publication of his new species, it is not true that *C. ancashiana* always has eglandular leaflets.

41. **Caesalpinia placida** *Brandegee* in Proc. Calif. Acad., Second Series, 3: 131 (1891). Type: Baja California, La Paz, 4 Feb. 1890, *Brandegee* s.n. (lectotype UC!, chosen here, isolectotype GH!).

Poinciana placida (Brandegee) Rose in Contribs. U.S. Nat. Herb. 13: 303 (1911).

Poincianella placida (Brandegee) Britton & Rose in N. Amer. Fl. 23(5): 331 (1930).

Unarmed, multiple-stemmed shrub (sometimes scrambling up through taller plants), 1--4 m tall, with slender (up to 2 cm in diam.) dark basal stems; bark shades of grey, smooth; foliage and inflorescences arising from woody brachyblasts; young stems reddish, ± zig-zag, glabrous or sparsely to moderately pubescent, densely glandular with red stipitate-glands. *Leaves* bipinnate; stipules ovate-orbicular, concave, finely pubescent, margins glandular fimbriate, caducous; petiole 4--12 mm long, glandular with sessile and stipitate glands intermixed, the stalks of the stipitate pixie-cup glands usually pubescent; rhachis (when present) 3--5 mm long, stipitate-glandular; pinnae in 1--2 opposite pairs, usually plus a terminal pinna but this occasionally lacking; leaflets in (3--)4--6(--7) opposite pairs per pinna, somewhat fleshy, oblong-elliptic to oblong-obovate, slightly falcate, apex rounded to emarginate, base inequilateral, oblique, margin ± crenulate, terminal leaflets 3.5--5 x 1.2--2 mm, medians c 3--7 x 1--2.5 mm, both surfaces glabrous; usually only the excentric main vein evident (the leaflet blade divided 2:1), occasionally one or two lateral veins visible on dried material; dark sunken glands in leaflet margin indentations, either in basal $^1/_2$ or around entire margin, undersurface of blade sparsely to densely glandular with dome-shaped, sessile or partially sunken glands. *Inflorescence* a 6--20-flowered terminal or lateral (arising from lateral brachyblasts) raceme, rhachis sparsely puberulous, glabrescent, stipitate-glandular; bracts yellow with red apices, ovate, 6--7 x 4--5 mm, apex acute or obtuse, margin fimbriate-glandular, surface sparsely pubescent and densely stipitate-glandular, caducous; pedicels 4--14 mm long, the base sits on a rhachis ledge resulting from fallen bract, articulated exactly below to 3 mm below tapered calyx base. *Calyx* tube red, ribbed, finely pubescent, stipitate-glandular, lobes red (yellow where they overlap in bud); c 7 mm long, reflexed on open flowers, margins fimbriate-glandular, surfaces densely stipitate-glandular, lower lobe ± cucullate. *Corolla* bright egg-yolk yellow, standard blade panduriform, 11--15 x 5--7.5 mm (including a 2--2.5 mm claw), reflexed, with indentations on margin at point of reflexion, orange stipitate-glandular on basal $^2/_3$ of dorsal face but not on claw which has a small tuft of white hairs at base on inner surface, covering staminal fenestrae; upper lateral petals oblong-obovate to broadly triangular, apex emarginate to obcordate, 11--15 x 5--11.5 mm (including a 1.5 mm claw); lower laterals as for upper ones in shape, 10.5--14.5 x 4.5--9.5 mm (including a 1.5 mm claw), the dorsal surfaces of the lateral petal blades stipitate-glandular on the

basal $^1/_3$ (the lower ones less so than the upper ones), claws sparsely pubescent, eglandular. Stamen filaments yellowish-green, 6.5--9 mm long, spreading pubescent on basal $^1/_2$--$^2/_3$, the hairs flattened, transparent (like wrinkled cellophane); anthers ochre to yellowish-orange, 1--1.5 x 0.5--0.75 mm. Ovary pubescent with short patent white hairs, especially along the upper margin, densely stipitate-glandular with mushroom-shaped glands; style 6--8 mm long, slightly curved at apex; stigma a terminal, tubular to slightly flared, fringed chamber. *Fruit* a coriaceous, ± falcate (curved upwards near apex), elastically dehiscent pod, 3.2--5 x 1--1.4 cm, valves twist after dehiscence, sparsely pubescent, glabrescent, stipitate-glandular with dark red mushroom-shaped or pixie-cup glands, (1--)3--5-seeded. *Seeds* ovate, 8 x 5 mm (immature). *Seedling* germination phaneroepigeal, cotyledons foliaceous, cordate at base, first eophyll pinnate with 4--5 pairs of opposite leaflets, second eophyll bipinnate with 1 pair of pinnae plus a terminal pinna, each with 3--4 pairs of opposite leaflets, hypocotyl glabrous, epicotyl purplish-red, stipitate-glandular. (Figs. 5V, **61** & 62 A & B, Map 5).

DISTRIBUTION. Endemic to Southern Baja California.

BAJA CALIFORNIA: La Paz, 4 Feb. 1890, *Brandegee* 167 (lectotype UC!, isolectotype GH!); E side of Bahia La Paz, 19 Oct. 1981, *Burgess & Turner* 6186 (MEXU!); c 6 km SSW of Loreto, 8 Oct. 1964, *Carter & Ferris* 4709 (NY!); Sierra de la Giganta, Arroyo Gabilán, 3 April 1960, *Carter & Ferris* 4071 (MEXU!, TEX!); N side of Arroyo Gabilán, nr. Rancho Rincón, 25 Nov. 1974, *Carter* 5875 (NY!); 6 km E of La Paz on road to Pichilingue, 28 Feb. 1990, *Contreras* 2725 (K!); 2--3 miles NE of La Paz, 7 May 1952, *Gentry & Fox* 11871 (LL!); 8 km E of La Paz on coastal road to Pichilingue, 18 Jan. 1992, *Lewis et al.* 2032 (BM!, FCME!, FHO!, K!, MEXU!, MO!, NY!, TEX!); 5 km E of La Paz, 18 Jan. 1992, *Lewis et al.* 2031 (FCME!, FHO!, K!, MEXU!, SI!); 15.8 km W of La Paz at turn-off to San Juan de la Costa,22 Jan. 1992, *Lewis et al.* 2046 (FCME!, FHO!, K!, MEXU!); La Paz, 7 Feb. 1928, *Jones* 24066 (F!, NY!); 4.2 miles E of La Paz on highway 11 to Pichilingue, 5 Sept. 1985, *Luckow* 2876 (MEXU!, NY!, TEX!); Espiritu Santo Is., 7 Feb. 1906, *Nelson & Goldman* 7499 (NY!); La Paz, 20 Jan.--5 Feb. 1890, *Palmer* 95 (F!, K!, NY!); 10.3 miles W of La Paz, 31 Dec. 1958, *Porter* 139 (MEXU!, TEX!).

ECOLOGY. Low cactus scrub on rocks, desert scrub on gravelly wash of arroyo, sedimentary and volcanic slopes with sparse shrub and tree cover, c 20--100(--200) m.

PHENOLOGY. Flowering September to May, fruiting October to May.

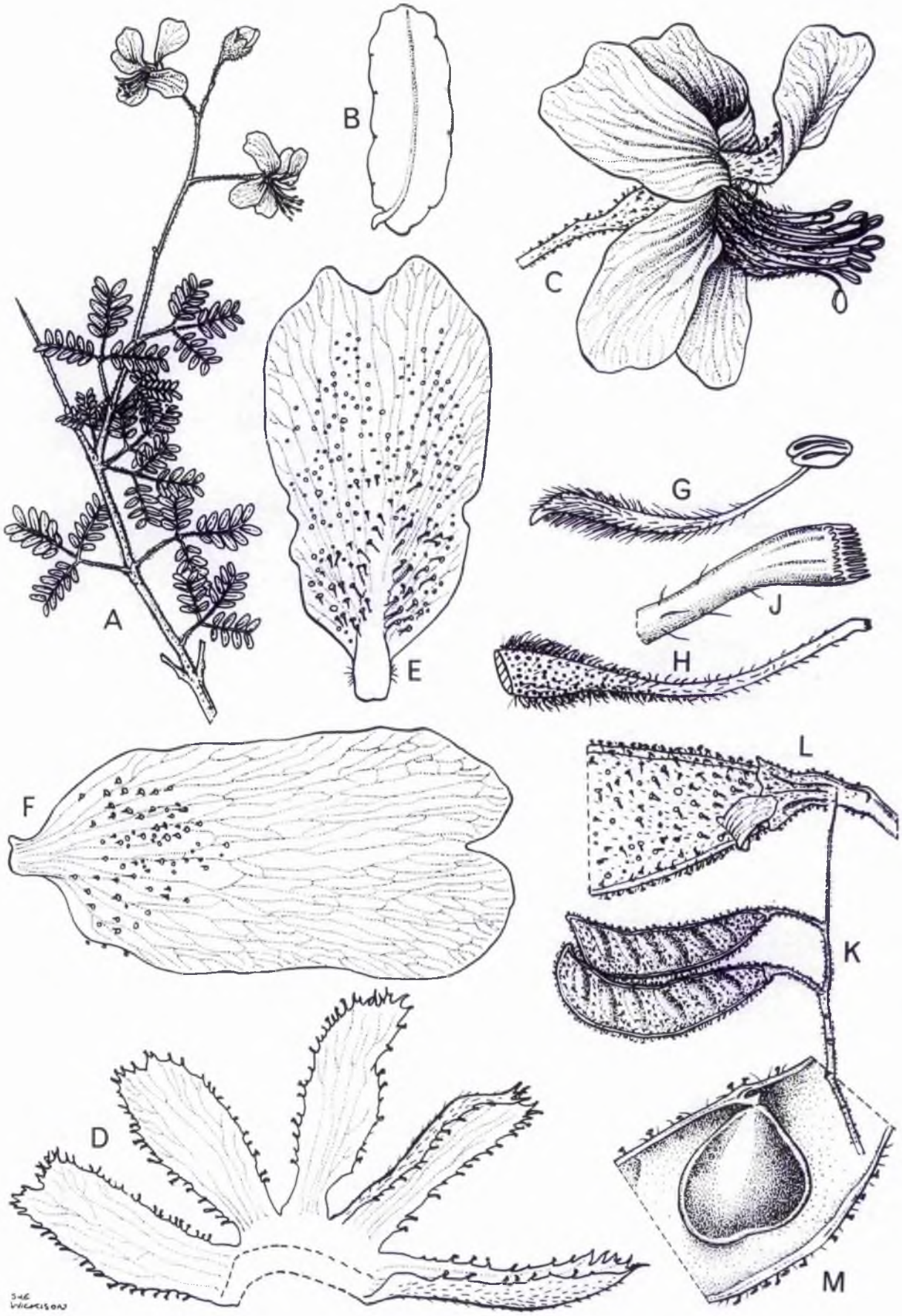


FIG. 61. *Caesalpinia placida*. **A** inflorescence and foliage x 1; **B** leaflet undersurface x 9; **C** flower x 4½; **D** calyx opened out x 6; **E** standard petal outer surface x 9; **F** upper lateral petal outer surface x 9; **G** stamen x 9; **H** gynoecium x 9; **J** stigma x 42; **K** fruits x 1; **L** detail of glands on fruit x 4½; **M** seed x 6. **A–C** from *Carter* 5875, **D–J** from *Palmer* 95, **K–M** from *Contreras* 2725. Drawn by Sue Wickison.

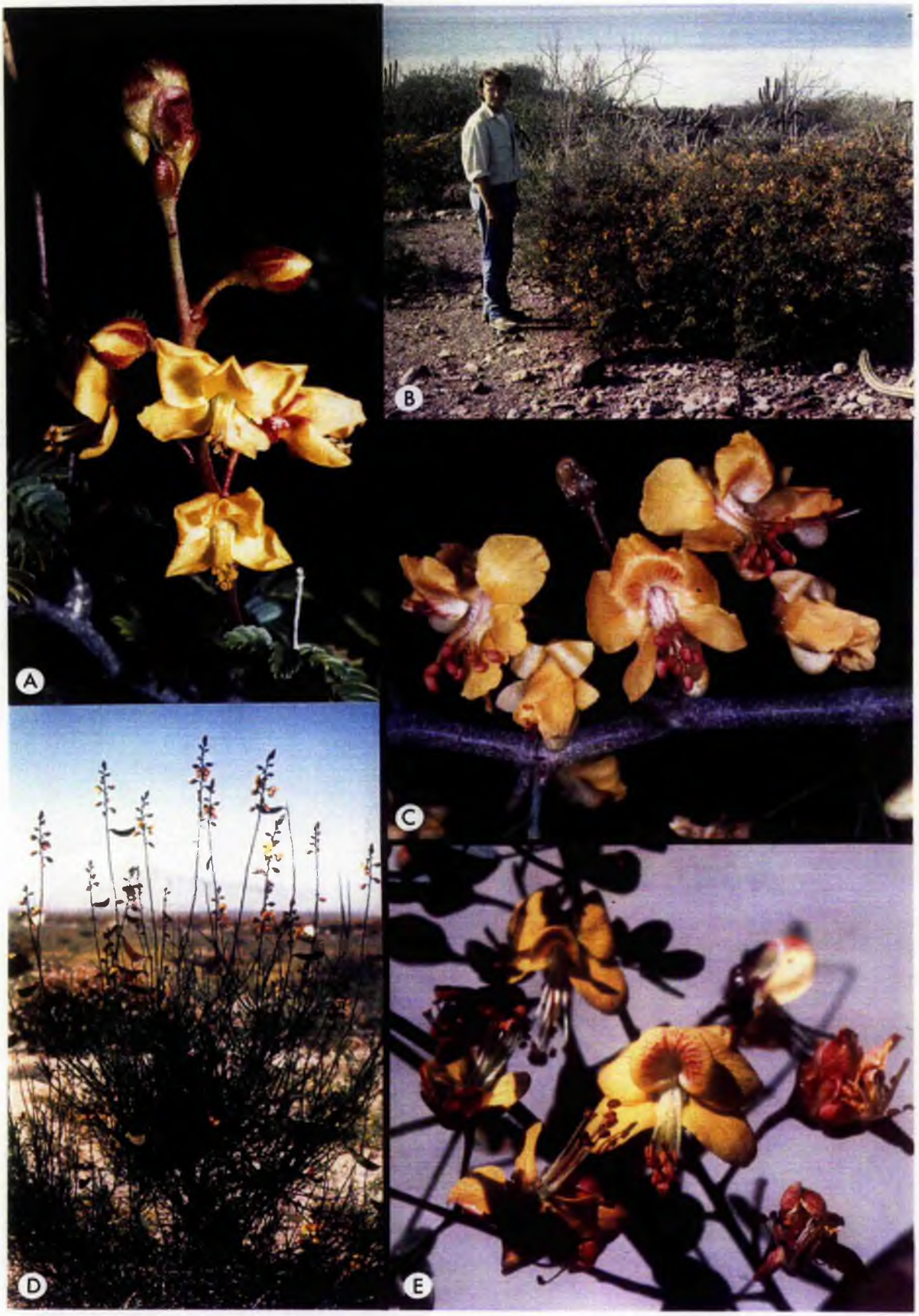


FIG. 62. *Caesalpinia placida*: **A** inflorescence (*Lewis et al.* 2031); **B** habit and habitat, Baja California (*Lewis et al.* 2032), C.E. Hughes for scale); *Haematoxylum brasiletto*: **C** flowers (*Lewis & Hughes* 1711); *C. angulata*: **D** habit, Chile (photo.: B.B. Simpson); *C. nelsonii*: **E** flowers (*Lewis et al.* 1794, photo.: C.E. Hughes).

NOTES. Brandegee (1891), when describing *C. placida*, numbered the species 167 in his list of taxa from the Cape Region of Baja California and commented that 'it blossoms in February' and is 'common about La Paz and [was] also collected there by Dr Palmer'. The supposed holotype, borrowed from UC, consists of two elements both numbered 167. The larger, flowering specimen, on the left hand side of the sheet was collected on 4 February 1890; the smaller, fruiting branchlet, on 1 November of the same year. The sheet thus represents two distinct collections and I have selected the left hand, flowering portion as the lectotype of *C. placida*. The right hand, fruiting material, evidently referred to in the protologue is a paratype.

Flowers are sweetly scented of orange blossom. The panduriform standard petal and crenulate-margined, glandular leaflets suggest that the closest relatives of *C. placida* are to be found in South America, for example species such as *C. trichocarpa* and *C. mimosifolia* from Argentina and Bolivia have many characters in common.

42. **Caesalpinia exilifolia** *Griseb.*, Plant. Lorentz: 80 (1874). Type: Argentina, Catamarca, near San José, 4 Jan. 1872, *Lorentz* 353 (holotype GOET!).

Unarmed shrub, 0.6--1 m tall; stems glabrous and sparsely glandular. *Leaves* bipinnate; stipules broadly ovate to orbicular, c 0.5 mm long, scarious, margin fimbriate, ciliate, caducous; petiole 2--5 mm long, pubescent at base, or along upper edge for entire length, or glabrous, sparsely glandular; rhachis 4--8 mm long, glabrous, sparsely glandular, more so around insertions of pinnae axes; pinnae in 2--5 opposite to subopposite pairs plus a terminal pinna (occasionally ending in a pair); leaflets in 5--7(--8) opposite pairs, cordate or ovate, apex obtuse, 1.5--3 x 0.75--2 mm, glabrous, ± fleshy, venation obscure, eglandular, sometimes at least one short-stalked gland at base of each leaflet on pinna rhachis. *Inflorescence* a 10--30-flowered terminal raceme, rhachis puberulous, glabrescent, sparsely to moderately stipitate-glandular, especially near apex; bracts ovate, acute, 2--3 mm long, pubescent, fimbriate, the margin with some stipitate glands and/or the fimbriae gland-tipped, caducous; pedicels 4--5(--9) mm long, puberulous, densely glandular with stipitate, pixie-cup glands, articulated just below or up to 1.5 mm below calyx. *Calyx* lobes 7--8(--9) mm long, outer surface pubescent, sessile

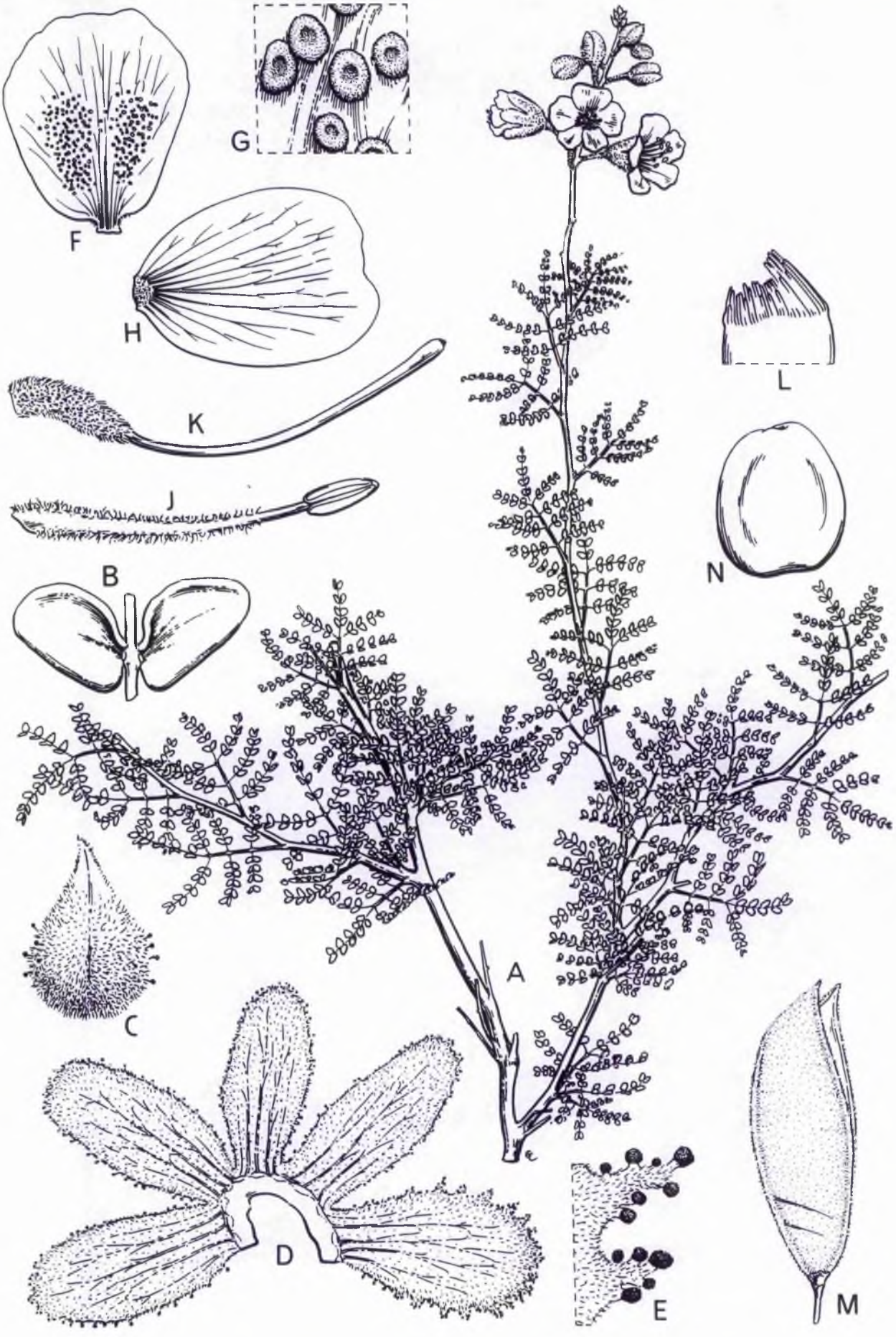


FIG. 63. *Caesalpinia exilifolia*. **A** habit x 1; **B** leaflets undersurface x 9; **C** bract x 15; **D** calyx opened out x 4½; **E** calyx lobe margin x 24; **F** standard petal dorsal surface x 4½; **G** glands on dorsal surface of standard petal x 60; **H** upper lateral petal x 4½; **J** stamen x 9; **K** gynoecium x 9; **L** stigma x 30; **M** fruit x 1½; **N** seed x 4½. **A–L** from *Krapovickas & Cristobal* 20588, **M & N** from *Schreiter* 46501. Drawn by Eleanor Catherine.

and stipitate pixie-cup glands on and close to the margins but not over entire surface, usually dense on the fimbriate margins, lower lobe cucullate, the entire outer surface pubescent and stipitate-glandular, the glands larger than on the other 4 lobes. *Corolla* yellow; standard petal spotted red, its blade obovate, 10 x 8 mm (including a 0.5 mm claw), dorsal surface of blade sessile-glandular, a small pubescent tuft at base of blade just above claw on inner surface; upper lateral petals obovate-elliptic, 10 x 8 mm (claw lacking) equalling standard in shape and size but thinner and eglandular, a small pubescent tuft at base; lower lateral petals obovate to oblanceolate, 11 x 6--7 mm (claw lacking), eglandular, a small pubescent tuft at base. Stamen filaments 7--8 mm long, basal $^1/_2$--$^2/_3$ pubescent, the reflexed hairs becoming sparse towards apex; anthers 2 x 1 mm. Ovary densely lanate, sessile glands along both margins, 7--8-ovulate; style 7 mm long; stigma a terminal, tubular, fringed chamber. *Pod* chartaceous to thinly woody, elastically dehiscent, 3.8--5.5 x 1.2--1.3 cm, pubescent, 2--6-seeded. *Seeds* dark brown, speckled and virtically streaked black, broadly ovate, 7--8 x 6 x 1.5--2 mm. (Figs. 5U & **63**, Map 20).

DISTRIBUTION. Endemic to NW Argentina.

ARGENTINA: Prov. Salta, Depto. Cafayate, 7 km S of Cafayate on route 40, 2 Jan. 1972, *Krapovickas & Cristóbal;* 20588 (F!, MBM!); Prov. Catamarca, San José, 4 Jan. 1872, *Lorentz* 352 (F (photo)!); Prov. Salta, road between Cafayate and Tres Cruces, 14 Jan. 1970, *Meyer & Legname* s.n. (NY!); Prov. Tucuman, Depto. Trancas, Las Arcas, 3 Feb. 1927, *Schreiter* 4735 (F!); Catamarca, Depto. Santa Maria, 8 km on road to Minas Capillitas from turn-off Route 40, 17 Jan. 1986, *Simpson* 1--7--86--1 (TEX!).

ECOLOGY. 1600--2000 m.

PHENOLOGY. Reported (Burkart 1936) to flower from November to May. I have seen flowering and fruiting specimens collected in January and February.

43. **Caesalpinia argentina** *Burkart* in Rev. Argent. Agron. 3: 105 (1936). Type: Argentina, Jujuy, Santa Cornelia, Sierra de Santa Bárbara, Nov. 1911, *Spegazzini* 2159 (holotype? LPS, n.v.).

Caesalpinia coulterioides Griseb. in Symb. Fl. Argent.: 113 (1879), pro parte.

Unarmed multiple-stemmed shrub to 2.5 m tall, young stems green with pale lenticels, finely pubescent with white hairs or densely velutinous, stipitate glands irregularly scattered amongst the hairs. *Leaves* bipinnate; stipules ovate to suborbicular or broadly triangular, 3--5 x 2--4 mm, obtuse, velutinous, the margin fimbriate, persistent; petiole 1.2--4 cm long; rhachis 4--13.5 cm long, leaf axis pubescent with expanded, prickle-like glands intermixed; pinnae in 3--6 opposite pairs plus a terminal pinna; leaflets in 5--9 opposite pairs, the terminals broadly obovate to elliptic, 5--20 x 3--7.5 mm, the medians oblong, oblong-elliptic to ovate, 6--24 x 4--10 mm, all leaflets with upper surface short-pubescent with white hairs, lower surface more densely pubescent with white, crinkled hairs, midvein prominent on lower surface, secondary venation obscure, glands on lower surface submarginal, ± regularly spaced, sunken or flush with blade surface. *Inflorescence* a ± 40--60-flowered, 6--20 cm long, terminal or leaf-opposed raceme, the rhachis velutinous and stipitate-glandular; bracts ovate-lanceolate, 5--12 mm long, acuminate, fimbriate, glandular; pedicels c 5--10 mm long, articulated just below calyx. *Calyx* lobes 7--12 mm long, the lower lobe cucullate, the surface velutinous and glandular, margin glandular-fimbriate. *Corolla* yellow; standard petal red, its blade elliptic, 13 x 8.5 mm (including a 1 mm claw), eglandular or with a few glands on the dorsal face, a few hairs on the claw margins; upper lateral petals ± obovate, 11 x 6.5 mm; lower lateral petals narrowly obovate, 13 x 5 mm. Stamen filaments c 10 mm long, pubescent on basal $^1/_2$--$^2/_3$, especially the ones on either side of the vexillary stamen; anthers 2 x 1 mm. Ovary densely pubescent, eglandular or almost so, 6--7-ovulate; style 4.5 mm long; stigma a terminal, funnel-shaped, fringed chamber. *Pod* chartaceous to thinly woody, elastically dehiscent, 5.8--9 x (1.3--)1.6--1.8(--2) cm, essentially eglandular but for a few short-stalked glands on margin near base, 4--7-seeded. *Seeds* olive-brown, shiny, ovate to subquadrate-elliptic, 7.5--10(--13) x 6--9 x 1--2 mm. (Fig. **64**, Map 22.)

DISTRIBUTION. Southern Bolivia and northern Argentina.

BOLIVIA: Rio Parapeti, 29 Aug. 1949, *Brooke* 5566 (F!, NY!); near Villa Montes, Rio Pilcomayo, Nov. 1910, *Herzog* 1121 (M!); Prov. Las Salinas, between Buyuyu and Itau, 1886, *Hieronymus & Lorentz* 953 (F, photo!); Depto. Tarija, road Tarija to Villa Montes, Bajada de Chimeo, 25 May 1971, *Krapovickas et al.* 19222 (MBM!); Depto. Chuquisaca, Prov. Azero, 5 km N of Carandaytí, 12 April 1977, *Krapovickas & Schinini* 31244 (F!); Depto. Santa Cruz, Prov. Cordillera, 14 km NW of Boyuibe, 14 April 1977,

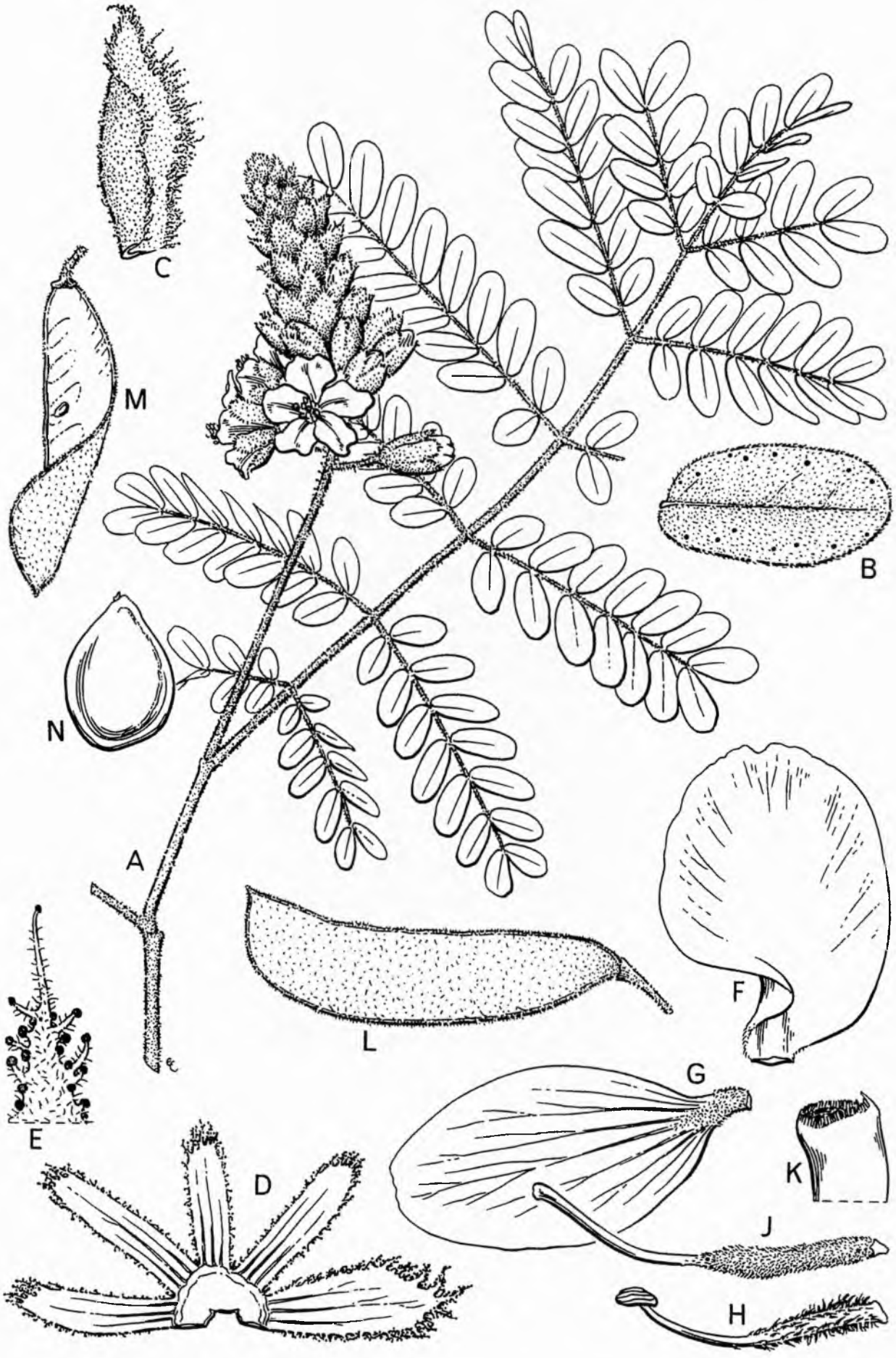


FIG. 64. *Caesalpinia argentina*. **A** inflorescence and bipinnate leaf x 1; **B** median leaflet undersurface x 3; **C** bract x 4½; **D** calyx opened out x 3; **E** calyx lobe detail x 15; **F** standard petal x 4½; **G** lateral petal x 4½; **H** stamen x 4½; **J** gynoecium x 4½; **K** stigma x 30; **L** fruit x 1; **M** single twised fruit valve x 1; **N** immature seed x 3. **A–K** from *Krapovickas et al.* 19353, **L** from *Cabrera* 4106, **M & N** from *Krapovickas & Schinini* 31325. Drawn by Eleanor Catherine.

Krapovickas & Schinini 31325 (MBM!, MO!); Depto. Tarija, Villa Montes, 28 May 1971, *Krapovickas et al.* 19353 (F!, MO!); Depto. Santa Cruz, Prov. Andres Ibanez, 80 km S of Santa Cruz, 24 Nov. 1990, *Pennington et al.* 13322 (K!); *Pennington et al.* 13323 (K!); ARGENTINA, Depto. Santa Bárbara, Laguna de la Brea, 9 July 1937, *Cabrera* 4106 (F!, NY!); Jujuy, Santa Cornelia, Sierra de Santa Bárbara, Nov. 1911, *Spegazzini* 2159 (LPS).

ECOLOGY. Roadside wasteground and transition vegetation to chaco.

PHENOLOGY. Flowering and fruiting April to August.

VERNACULAR NAME. "Camiri" (Bolivia).

44. **Caesalpinia coluteifolia** *Griseb.*, Symb. ad Flor. Arg.: 111 (1879). Type: Argentina, Tucumán, near El Alduralde on the route to Salta, Feb. 1873, *Lorentz & Hieronymus* 1004 (holotype GOET!, isotype CORD, n.v.).

Unarmed multiple-stemmed shrub, 1--1.5 m tall; young stems puberulous, older stems glabrescent, eglandular or very sparsely stipitate-glandular. *Leaves* bipinnate; petiole 1--1.9 cm long, pubescent, stipitate-glandular near base or along entire length; rhachis 2.5--5.5 cm long, glabrous; pinnae in 2--4 opposite pairs plus a terminal pinna; leaflets in 2--4 opposite pairs, terminals obovate to elliptic, 10--20 x 6--14 mm, medians elliptic to broadly ovate, 7--18 x 4--10.5 mm, all leaflets with both surfaces glabrous, midvein prominent on lower surface, secondary venation not visible, blades eglandular, a few short-stalked glands at the pinnae and leaflet petiolule insertions, the gland stalks pubescent. *Inflorescence* a 15--c 60-flowered, terminal raceme, up to c 18 cm long, rhachis puberulous or pubescent, eglandular or densely stipitate-glandular; bracts ovate, acute to acuminate, 4--7 mm long, pubescent, fimbriate, the fimbriae often gland-tipped, glandular near the margins, caducous; pedicels 5--9 mm long, puberulous, eglandular or densely stipitate-glandular with pixie-cup glands, apparently unjointed. *Calyx* upper 4 lobes c 8--10 mm long, the outer faces pubescent, margins fimbriate, ciliate, fimbriae gland-tipped, lower lobe 11 mm long, much broader than other 4 lobes. *Corolla* yellow; standard petal veined intense red-orange, blade obovate, 9 x 6--8 mm (including a 1 mm claw), outer surface of blade densely glandular with subsessile mushroom-shaped glands, the gland heads distinctly larger near petal claw than near apex, basal $^2/_3$ of blade inner

FIG. 65. *Caesalpinia coluteifolia*. **A** habit x 1; **B** median leaflet undersuface x 3; **C** bract x 4½; **D** calyx opened out x 3; **E** calyx lobe margin x 30; **F** standard petal front view x 4½; **G** standard petal side view x 4½; **H** detail of standard petal glands x 24; **J** lateral petal x 4½; **K** stamen x 4½; **L** gynoecium x 4½; **M** stigma x 30; **N** eglandular fruit x 1; **P** glandular fruit x 1; **Q** twisted fruit valve x 1; **R** seed x 3. **A** & **B** from *Venturi* 5446 (with inflorescence from *Schinini & Borda* 16417), **D–M**, **Q** & **R** from *Beck & Liberman* 9442, **N** from *Deroto & Alberti* 3102, **C** & **P** from *Schinini & Borda* 16417. Drawn by Eleanor Catherine.

surface and claw inner surface and margins densely pubescent; upper lateral petals oblanceolate to elliptic, 9--10 x 4.5--6 mm (including a 1 mm claw); lower laterals oblanceolate, 9--10 x 4--4.5 mm (including a 1 mm claw), all 4 laterals with claw margin and inner surface pubescent, one or two glands on margins. Stamen filaments 10--11 mm long, densely pubescent on basal $^1/_2$, less so toward apex, one stamen on either side of vexillary stamen with a densely pubescent thickened base; anthers 2 x 1 mm, very slightly apiculate. Ovary densely pubescent on base and upper margin with small sessile and stipitate pixie-cup glands intermixed, sometimes densely glandular, the gland heads larger on glands on upper margin; style c 11 mm long (much shorter on "male" flowers with reduced pistils); stigma a terminal, tubular, fringed chamber. *Pod* coriaceous to thinly woody, elastically dehiscent, 4.2--6.7 x 1.2--1.5 cm, sparsely to moderately pubescent, glabrescent, eglandular but for a few glands at base or moderately stipitate-glandular, 5--6(--7)-seeded. *Seeds* pale brown, shiny, ovate-cordate, 8 x 7 x 1.5--2 mm. (Fig. **65**, Map 22.)

DISTRIBUTION. Paraguay and Argentina.

PARAGUAY: Depto. Nueva Asuncion, 13 km towards Mariscal Estigarriba, 5 Oct. 1983, *Beck & Liberman* 9442 (NY!); Nueva Asuncion, ruta Trans-Chaco, 7 March 1979, *Schinini & Borda* 16417 (NY!); **ARGENTINA**, Prov. Salta, Depto. Gral Güemes, 34 km N of Rio Juramento, 3 Nov. 1974, *Burkart et al.* 30483 (K (photo)!, TEX!); Prov. Salta, Jaquiasme, 22 Dec. 1938, *Deroto & Alberti* 3102 (K!); Prov. Salta, Dep. Güemes, Juramento, 22 March 1977, *Krapovickas & Schinini* 30442 (F!); Salta, without date, *Lorentz* s.n. (K!); Rio Juramento, Feb. 1873, *Lorentz & Hieronymus* 273 (F!); Tucamán, Depto. Trancas, 3.7 km E of turn-off Route 9 to San Vicente, 28 Jan. 1986, *Simpson* 1--28--86--2 (TEX!); Balcogua, 16 Jan. 1928, *Venturi* 7091 (F!); Trancas, Zapia, 12 Dec. 1920, *Venturi* 1117 (F!); Depto. Capital, ? El Cadillal, 26 Oct. 1927, *Venturi* 5446 (K!).

ECOLOGY. Shrubby woodland on sand, 410--1250 m.

PHENOLOGY. Flowering and fruiting October to March.

VERNACULAR NAME. "Parolillo" (Argentina).

NOTES. Closely related to *C. exilifolia* but with consistently larger leaflets.

45. **Caesalpinia coulterioides** *Griseb.* emend. *Burk.* in Rev. Argent. Agron. 3: 97 (1936). Type: Argentina, Jujuy, Depto. Tumbaya, El Volcán, 12--13 May 1873, *Lorentz & Hieronymus* 760 (holotype GOET, n.v., isotype CORD, n.v.).
Caesalpinia coulterioides Griseb., Symb. ad Flor. Arg.: 113 (1879), (as "*coulteriodes*"), pro parte quoad material from El Volcán.

Unarmed shrub to 2 m tall; stems pubescent and stipitate-glandular, the gland stalks often hairy. *Leaves* bipinnate; stipules ovate-orbicular to cordate, 10--12 x 10--13 mm, apex rounded, base cordate-auriculate, outer surface glabrous, sparsely to moderately stipitate-glandular, inner surface puberulous, margins dentate-fimbriate, glandular, ± persistent; petiole 2.5--6.3 cm long, pubescent, stipitate-glandular, rhachis 9.5--20.5 cm long, pubescent, stipitate-glandular; pinnae in 5--11 opposite to subopposite pairs plus a terminal pinna (less often ending in a pair); leaflets in (8--)9--13 opposite pairs, oblong-elliptic, the terminals 10--12 x 5--5.5, the medians 12.5--16.5 x 4.5--6 mm, both surfaces glabrous, fleshy, midvein prominent on lower surface, other venation obscure, lower surface punctate-glandular along margin, glands sometimes restricted to leaflet apex, more often concentrated along distal margin of leaflet, occasionally sparsely scattered along entire margin, less often the margin crenulate with glands in the sinuses, a dentate corona of gland-tipped appendages on the leaf rhachis around the pinnae insertions. *Inflorescence* a 25--40-flowered terminal raceme; rhachis, pedicels and calyx tube pubescent and densely stipitate-glandular or rhachis pubescent and sparsely glandular, pedicels and calyx tube puberulous and eglandular; bracts lanceolate-ovate, acute to acuminate, c 10--12.5 mm long, outer surface pubescent and glandular, margin fimbriate-glandular, caducous; pedicels c 8--9(--12) mm long, articulated 1--3 mm below calyx (articulation often obscure). *Calyx* lobes 10--11 mm long, outer surfaces glandular, margins fimbriate with fimbriae gland-tipped, lower lobe 11--12.5 mm long. *Corolla* red; standard petal blade oblanceolate, 15--18 x 10--11 mm (including a 2.5--3 mm claw), blade eglandular, inner surface at base and margin of claw puberulous; upper lateral petals obovate to oblanceolate, 15--17 x 7--11 mm (including a 0.5--2.5 mm claw), eglandular, blade base and claw margin sparsely puberulous; lower laterals oblanceolate, 15.5--17 x 5.5--8 mm (including a 0.5--3 mm claw), eglandular, claw very sparsely puberulous. Stamen filaments 18--22 mm long, pubescent on basal $^1/_2$--$^2/_3$, becoming glabrous towards apex;

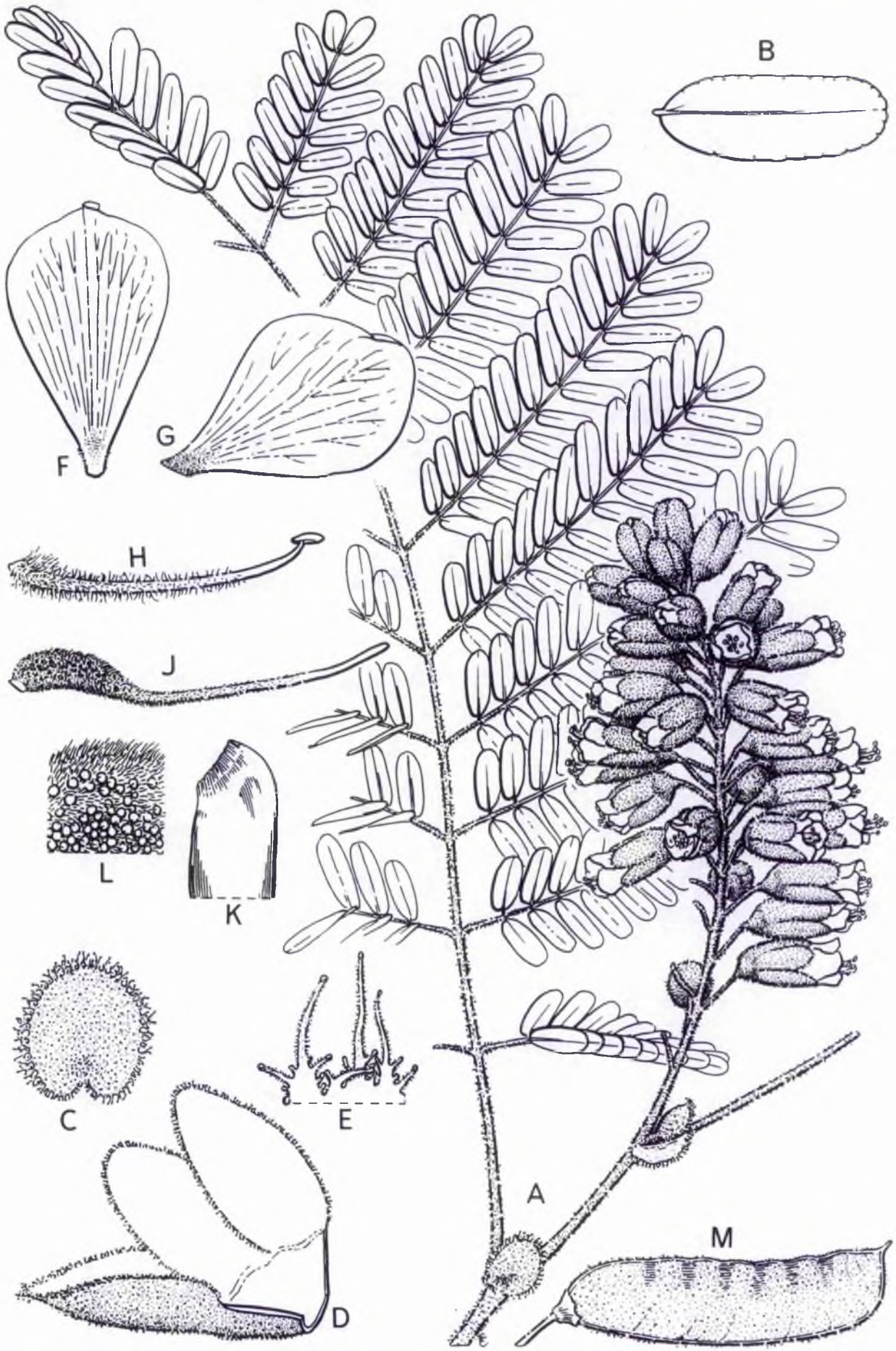


FIG. 66. *Caesalpinia coulterioides*. **A** part bipinnate leaf and inflorescence x 1; **B** leaflet undersurface x 3; **C** stipule x 2¼; **D** ½ calyx opened out x 3; **E** calyx lobe detail x 15; **F** standard petal x 3; **G** upper lateral petal x 3; **H** stamen x 3; **J** gynoecium x 3; **K** stigma x 30; **L** detail of ovary glands x 15; **M** fruit x 1 . All from *Fiebrig* 2443. Drawn by Eleanor Catherine.

anthers 2--2.5 x 1 mm. Ovary pubescent, sometimes densely so, sparsely to densely pixie-cup glandular; style 18--22 mm long, pubescent on basal $^1/_2$--$^2/_3$; stigma a terminal, tubular, fringed chamber. *Pod* coriaceous to subligneous, elastically dehiscent, 6.5--8.3(--9) x 1.6--2.2 cm, puberulous (the hairs most evident on the suture), glabrescent, stipitate-glandular or ± eglandular, (3--)6--7(--8)-seeded. *Seeds* ovate, c 11 x 7 x 2 mm. (Fig. 66, Map 22).

DISTRIBUTION. NW Argentina and southern Bolivia.

BOLIVIA: Tucumilla near Tarija, 30 Dec. 1903, *Fiebrig* 2443 (E!, K!, M!); **ARGENTINA**, Prov. Jujuy, El Volcán, Feb. 1922, *Castillon* s.n. (BR!); Prov. Jujuy, Depto. Captial, between León and Nevado de Chañi, March 1963, *Fabris et al.* 4245 (MBM!); Prov. Jujuy, Depto. Tumbaya, El Volcán, 14 Feb. 1927, *Venturi* 4973 (F!, NY!).

ECOLOGY. Mountain slopes, 2100--2800 m.

PHENOLOGY. Flowering and fruiting December to March.

46. **Caesalpinia angulata** (*Hook. & Arn.*) G.P. Lewis comb. nov., in sched.

Zuccagnia? angulata Hook. & Arn., Bot. Beechy's Voyage: 22 (1830). Type: Chile, Coquimbo (holotype ? E, n.v.).

Caesalpinia angulicaulis Clos, Fl. Chile: 223 (1846). Type: Chile, Coquimbo, Andacollo, near the Rio Hurtado (holotype ? TL, n.v.).

Unarmed sprawling shrub to 1 m tall with green, angular stems, young stems puberulous and ± densely glandular with short and long-stalked glands, older stems glabrous or glabrescent, eglandular. *Leaves* bipinnate; stipules lanceolate-triangular, c 3 mm long, margins glandular, lower portion ± clasping petiole; petiole 5--15 mm long; pinnae in 1--2 opposite pairs plus a terminal pinna (the terminal one longer than the laterals); leaflets in 4--7(--8) opposite pairs, oblong-elliptic to obliquely ovate or ± orbicular, apex acute, 3--6.5 x 1.5--4 mm, both surfaces glabrous, eglandular, ± fleshy, venation obscure, a small gland at the base of each petiolule. *Inflorescence* a 6--25-

flowered terminal raceme, the rhachis angular, ribbed, puberulous, densely stipitate-glandular with pixie-cup glands; bracts ovate-lanceolate, 7--10 mm long, acute to apiculate, pubescent, glandular; pedicels 4--9 mm long, articulated 1--1.5 mm below calyx. *Calyx* lobes 8--10 mm long, glandular, especially on the margins, lower lobe 12 mm long, cucullate, wider than the other 4, stipitate glands on outer surface, the margin glandular-fimbriate. *Corolla* golden yellow or orangish; standard petal ? suffused pinkish-red in centre, or spotted red, obovate to oblanceolate, 12.5--13 x 7--8 mm, outer surface with stipitate, mushroom-shaped glands; upper and lower lateral petals oblanceolate to narrowly obovate, 12--12.5 x 4.5--5 mm, the outer surface with sessile or stalked, mushroom-shaped glands, especially near the base, all petals lacking an obvious claw. Stamen filaments 8--10 mm long, pubescent on basal $^1/_2$--$^3/_4$, some filaments densely lanate near base; anthers 2 x 1--1.5 mm. Ovary densely white pubescent with stipitate, pixie-cup glands intermixed, style c 8 mm long (some flowers with a reduced, rudimentary ovary with a short style, the flowers thus functionally male); stigma a terminal, flared or funnel-shaped or tubular, fringed chamber. *Pod* chartaceous, elastically dehiscent,4--6.4 x 1.25--1.9 cm, sparsely pubescent with patent white hairs or glabrous, sparsely to moderately stipitate-glandular, (2--)3--5-seeded. *Seeds* pale brown, broadly ovate, 8 x 6 x 2 mm. (Figs. 62D & **67**, Map 22).

DISTRIBUTION. Endemic to Chile.

CHILE: 31 km N of Vallenar, 7 Feb. 1989, *Aronson* 7725 (K!); Carrizal, Aug. 1890, *Ball* s.n. (K!); Coquimbo, without date, *Beechy* s.n. (K!); Coquimbo, without date, *Bridges* 1292 (K!); Coquimbo, without date, *Cuming* 902 (K!); Coquimbo, Sept. 1927, *Elliot* 34 (E!, K!); without locality or date, *Gay* s.n. (K!); Prov. of Coquimbo, without date, *Gay* 140 (BR!, F!); Atacama Desert, 1885--7, *Geisse* 129 (NY!); without exact locality, ? Oct. 1871, *King* s.n. (E!); Coquimbo, Fray Jorge, 20 Oct. 1961, *Kubitzki* 103 (M!); without exact locality, without date, *Lobb* 444 (K!); Coquimbo, 1825, *Macrae* s.n. (K!); Prov. Coquimbo, Depto. La Serena, Cuesta de Pajonales, 16 Sept. 1957, *Ricardi & Marticorena* 4376/761 (F!); near La Serena, 10 Oct. 1914, *Rose & Rose* 19296 (NY!); Prov. Coquimbo, Fray Jorge, 3 Aug. 1917, *Skottsberg* 740 (F!); Depto. Ovalle, Fray Jorge, Nov. 1925 *Werdermann* 888 (A!, E!, F!, K!, M!); Prov. Atacama, Depto. Huasco, c 25--35 km N of Vallenar, on road to Copiapo, 29 Oct. 1938, *Worth & Morrison* 16269 (K!); Prov. Coquimbo, Depto. Elqui, c 6 km NW of Vicuna, Quebrada La Vinita, 3 Nov. 1938, *Worth & Morrison* 16364 (K!).

ECOLOGY. Desert scrub, 100--1000 m.

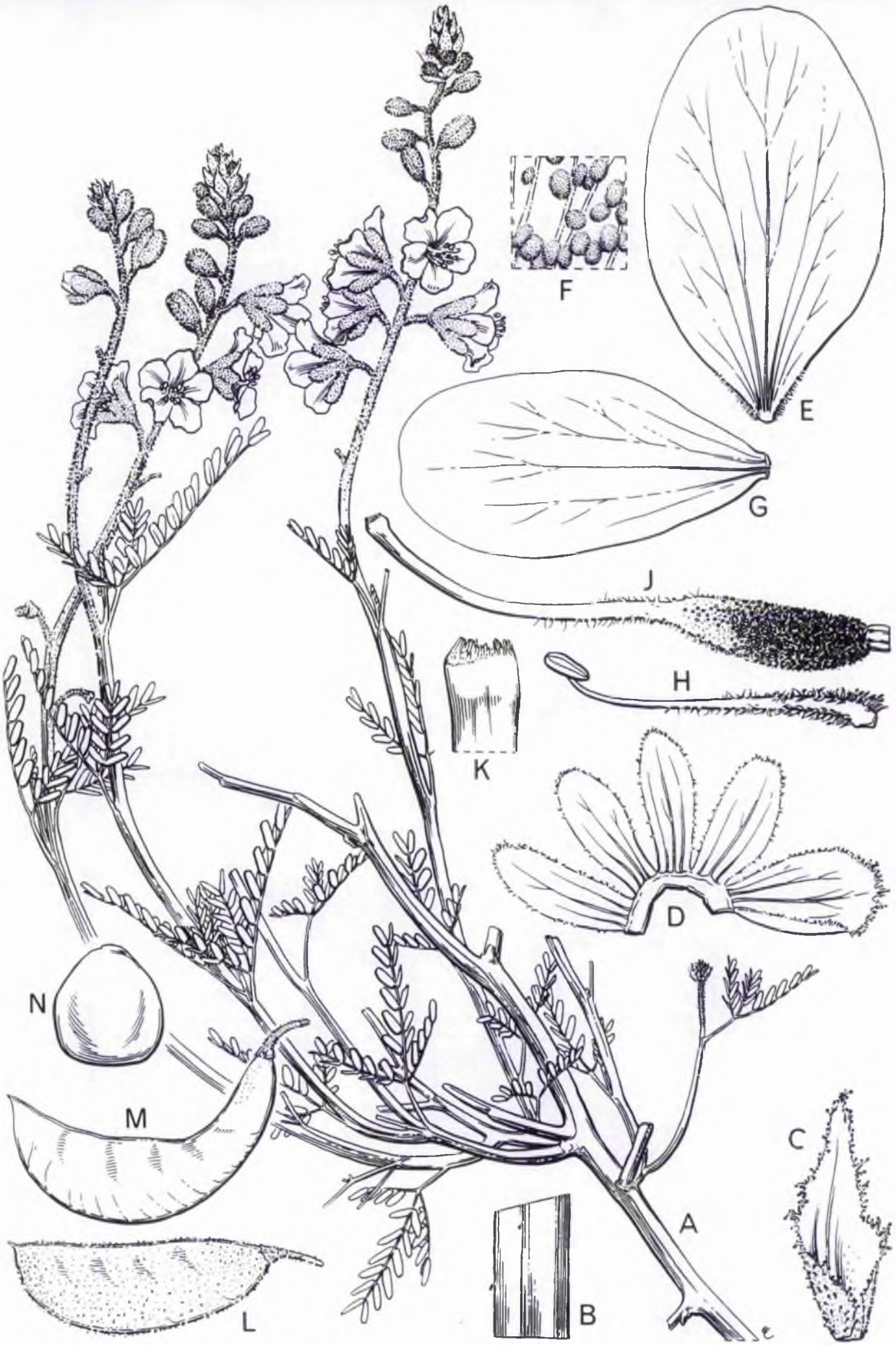


FIG. 67. *Caesalpinia angulata*. **A** habit x 1; **B** angular stem x 9; **C** bract x 6; **D** calyx opened out x 3; **E** standard petal x 6; **F** detail of glands on dorsal surface of standard petal x 22½; **G** lateral petal x 6; **H** stamen x 6; **J** gynoecium x 6; **K** stigma x 22½; **L** glandular fruit x 1; **M** glabrous fruit x 1; **N** seed x 3. **A–K** from *Ricardi & Marticorena* 4376/761, **L** from *Macrae* s.n., **M** from unknown collector 53, **N** from *Aronson* 7725. Drawn by Eleanor Catherine.

PHENOLOGY. Flowering and fruiting from (June-) August to February.

VERNACULAR NAME. "Yerba buena".

NOTES. The combination *Caesalpinia angulata* (Hook. & Arn.) Baillon, written on a few specimens, does not appear to have been validly published, nor have I found any manuscript bearing this name where the handwriting can be attributed to Baillon. It was thus necessary to make the combination *Caesalpinia angulata* (Hook. & Arn.) G.P. Lewis.

47. **Caesalpinia caudata** (*A. Gray) E.M. Fisher* in Bot. Gaz. 18: 123 (1893). Type: USA, Texas, between the Nueces and the Rio Grande, *Wright* 146 (holotype GH, n.v., isotype K!).

Hoffmannseggia caudata A. Gray in Bost. Journ. Nat. Hist. 6: 179 (1850).

Schrammia caudata (A. Gray) Britton & Rose in N. Amer. Flora 23(5): 317 (1930).

Unarmed, multiple-stemmed, woody-based perennial herb, up to 1 m tall, arising from thick woody rootstock; stems glabrous, sparsely glandular. *Leaves* bipinnate; stipules suborbicular, c 3 mm long, apex rounded, base auriculate, inner surface pubescent, margin ciliate and fimbriate-glandular, scarious, persistent; petiole 1.5--3 cm long, glabrous, sparsely glandular; rhachis 3--5 cm long, glabrous, sparsely glandular; pinnae in 2--4 opposite to subopposite pairs plus a terminal pinna which is distinctly longer than the lateral pinnae; leaflets in 3--7 opposite pairs on lateral pinnae, 8--20 pairs on terminal pinna, obliquely ovate, acute, apiculate, terminals 1--6 x 0.5--4 mm, medians 4.5--9 x 3.5--7 mm, both surfaces glabrous, fleshy, the margin thickened, main vein and secondaries prominent especially on lower surface, several secondaries arising from leaflet base, venation pattern essentially palmate with the secondaries brochidodromous; punctate, dark glands sparsely scattered over lower surface of blade or leaflet eglandular but for the gland-tipped apiculate apex, a gland-tipped appendage at the base of each petiolule insertion. *Inflorescence* a 6--15-flowered, axillary or terminal raceme, the rhachis glabrous or very sparsely pubescent, sparsely glandular; bracts ovate, acute, 3--4 mm long, pubescent and sparsely glandular; pedicels 5--8 mm long, crinkled-pubescent with white hairs, sessile and stipitate-glandular, unarticulated. *Calyx* lobes 7--7.5 mm long, outer surface crinkled-pubescent and glandular (most glands sessile), margins fimbriate-

glandular, lower lobe cucullate. *Corolla* yellow; standard petal blade broadly ovate, 8 x 8 mm (including a 0.5 mm claw); upper lateral petals broadly elliptic, 9--11 x 5.5--6 mm (including a 0.5 mm claw); lower laterals oblanceolate, 10.5--12 x 4.5--5 mm (including a 1.5 mm claw), all petals with glabrous blades and pubescent claw margins, all with outer surfaces densely glandular with sessile, subglobose (mushroom cap-shaped) glands. Stamen filaments 10--11 mm long, densely pubescent on the basal $^1/_3$--$^1/_2$, less so to glabrous on upper $^1/_2$, the hairs mostly reflexed; anthers 1.5 x 0.75 mm. Ovary densely lanate and at base densely sessile glandular or upper $^1/_2$ and upper margin densely pubescent, basal $^1/_2$ glandular; style 10--11 mm long; stigma a terminal, tubular or flared, fringed chamber. *Pod* chartaceous or coriaceous, elastically dehiscent, 2.4--4.6 x 1--1.6 cm, very sparsely pubescent, glabrescent, sparsely to moderately glandular with short-stalked or sessile glands, (1--)3--4-seeded. (Fig. **68**, Map 3).

DISTRIBUTION. USA in southwestern Texas and New Mexico (literature reference only), Mexico in Nuevo Leon and Tamaulipas.

MEXICO: Nuevo Leon, 26 mi E of General Bravo, 27 Nov. 1966, *Ripley & Barneby* 14783a (NY!); **Tamaulipas,** 24 km S of Nuevo Laredo, 24 March 1962, *Dominguez & McCart* 8206 (TEX!); near Nuevo Laredo, 29 March 1939, *Perkins & Hall* 3124 (F!); 37 mi S of Nuevo Laredo, 17 March 1962, *Rivas et al.* 8121 (TEX!); **USA: Texas,** Starr Co., 1 mi N of Viboras, 23 March 1962, *Alvarez et al.* 7905 (TEX!); Webb Co., Laredo, 11 June 1960, *Baird* s.n. (TEX!); Dimmit Co., c 11 mi NW of Carrizo Springs, 20 May 1987, *Barneby* 18213 (NY!); Webb Co., Laredo, 27 March 1956, *Bottimer* s.n. (TEX!); Duval Co., 53 mi NE of Laredo, 10 March 1962, *Bustamante & Bustamante* 77 (TEX!); Zapata Co., 20 mi NE of Zapata, 16 April 1962, *Cabrera* 128 (TEX!); 10 mi S of Zapata, 8 March 1963, *Cabrera* 74 (TEX!); Webb Co., 6 mi NE of Laredo, 16 March 1963, *Cisneros* 5 (LL!, TEX!); Zapata Co., 16 June 1933, *Clover* 1275 (NY!); Jim Hogg Co., 6 mi S of Petroleum on rd. to Guerra and Garceno, 28 June 1962, *Correll & Johnston* 25635 (LL!, MO!, NY!); Webb Co., 11 mi S of Laredo, 19 April 1959, *Correll & Rollins* 20934 (LL!, NY!); Dimmit Co., 12 mi NW of Carrizo Springs, 19 April 1966, *Correll & Rollins* 32555 (LL!, NY!); Carrizo Springs, 6 April 1930, *Hogland* s.n. (TEX!); Duval Co., 5 mi SW of Benavides, 13 April 1963, *Garcia* 122 (LL!); Zapata Co., 6 mi E of Zapata, 1 April 1963, *Garcia & Cuellar* 61 (LL!); 22 mi S of Laredo, 4 April 1965, *Guerra et al.* 612 (TEX!); Jim Hogg Co., 5 April 1940, *Hamby* 723 (LL!); 4.5 mi E of Hebbronville, 7 March 1954, *Johnston* 54126 (TEX!); Brooks Co., 10 mi N of Encino, 16 April 1954, *Johnston* 54495 (TEX!); Jim Hogg Co., 1942, *Lehmann & Davis* 41 (F!); Webb Co., 6 mi E of Laredo, 15 Nov. 1961, *Martinez & Trevino* 71 (TEX!); nr. Laredo, Aug. 1899, *Mackenzie* 68 (NY!); Zapata Co., 22 km S of Laredo, 3 April 1965, *Novoa & Cantu* 28 (TEX!); Dimmit Co., 5 mi N of Carrizo Springs, 16 March 1963,

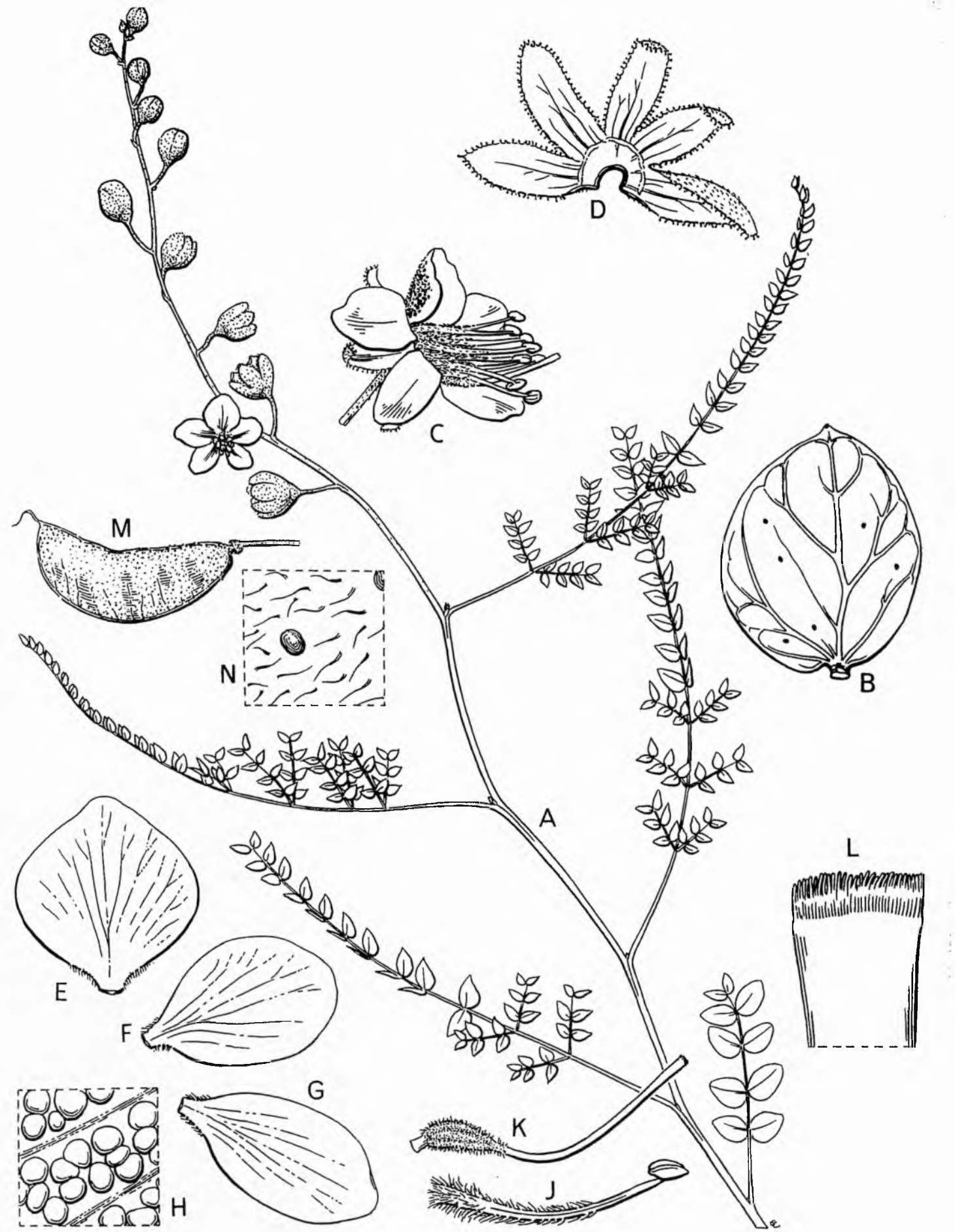


FIG. 68. *Caesalpinia caudata*. **A** inflorescence and foliage x 1; **B** leaflet undersurface x 7½; **C** flower x 2¼; **D** calyx opened out x 3; **E** standard petal x 4½; **F** upper lateral petal x 4½; **G** lower lateral petal x 4½; **H** detail of glands on petal dorsal surface x 30; **J** stamen x 4½; **K** gynoecium x 4½; **L** stigma x 45; **M** fruit x 1; **N** detail of fruit surface x 30. **B** from *Correll & Johnston* 25635, the rest from *Cisneros* 5. Drawn by Eleanor Catherine.

Noyola 38 (TEX!); Webb Co., 6 mi NW of Laredo, 25 March 1962, *Paez* 122 (TEX!); Laredo, 15 March 1917, *Palmer* 11273 (NY!); Starr Co., Rio Grande, Fort Ringgold, 20 April 1924, *Runyon* 600 (F!, K!,NY!, TEX!, US!); Cameron Co., nr. Brownsville, June 1925, *Runyon* 1079 (NY!); Rio Grande, 5 April 1852, *Schott* 279 (NY!); between Laredo and Ringgold Barracks, June 1853, *Schott* 131 (F!, NY!); Webb Co., 30 mi SE of El Indio, 20 April 1974, *Smith et al.* 27 (TEX!); 14 mi NE of Laredo, 18 April 1962, *Soto et al.* 8079 (TEX!); Starr Co., Rio Grande City, 16 June 1928, *Tharp* s.n. (TEX!); N of Rio Grande City, *Tharp* 5965 (TEX!); Zapata Co., 13.9 mi N of San Ignacio,19 May 1980, *Turner* 80--69 M (TEX!); Dimmit Co., nr. Carrizo Springs, 31 Aug. 1983, *Williges* s.n. (NY!, TEX!); Webb Co., nr. San Ildefonso Creek, 6 April 1966, *Wood* 716 (TEX!); Zapata Co., nr. Zapata, 30 April 1966, *Wood* 750 (TEX!); without exact locality, Oct. 1849, *Wright* 146 (K!).

ECOLOGY. Orange and red sands, sandy gravel or sandy loam in open grassy areas of mesquite savanna, one altitudinal record of 60 m.

PHENOLOGY. Main flowering and fruiting from March to June, one flowering record for August and fruiting records for October and November.

NOTES. In 1892 E.M. Fisher published a revision of the genus *Hoffmannseggia* in North America and included *H. caudata* A. Gray stating that the species "is related to *Caesalpinia* in respect to sepals, petals, and pod". One year later (Fisher 1893) he united *Hoffmannseggia* with *Caesalpinia* and provided new combinations in the latter for all the taxa, "even if extreme species in the two genera seem to be so unlike each other". Pivotal to his argument for doing this was *H. caudata* which he argued has more the characters of *Caesalpinia palmeri* S. Wats. than of any species of *Hoffmannseggia*. If Fisher had just transferred *H. caudata* to *Caesalpinia* that would have resolved the problem, but in moving all the species of *Hoffmannseggia* to *Caesalpinia* he perpetrated a taxonomic error that has confused all subsequent workers. Britton and Rose (1930) recognised the unique combination of characters that diagnosed the species and described a new genus, *Schrammia*, to accommodate it. The long terminal pinna which far exceeds the lateral pinnae in length and leaflet number is particularly diagnostic. The species is here recognised as the northern-most representative of the *Poincianella* group.

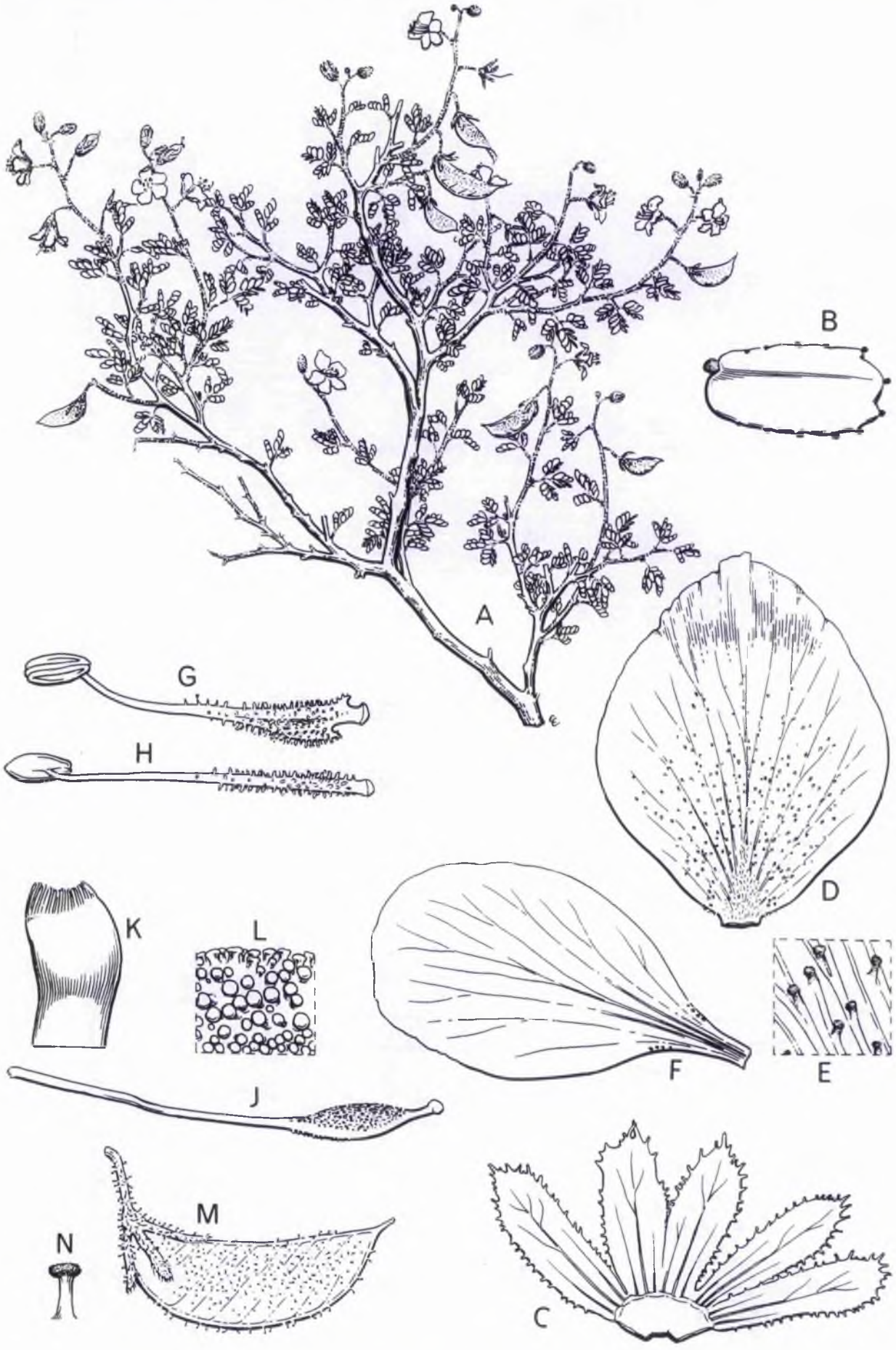


FIG. 69. *Caesalpinia pumilio*. **A**, habit x 1; **B** median leaflet undersurface x 12; **C** calyx opened out x 9; **D** standard petal x 12; **E** detail of glands on dorsal surface of standard petal x 45; **F** lateral petal x 12; **G** & **H** stamens x 12; **J** gynoecium x 12; **K** stigma x 45; **L** detail of glands on ovary x 45; **M** fruit x 3; **N** fruit gland x 45. **A**, **M** & **N** from *Cabrera* 30150, the rest from *Venturi* 8309. Drawn by Eleanor Catherine.

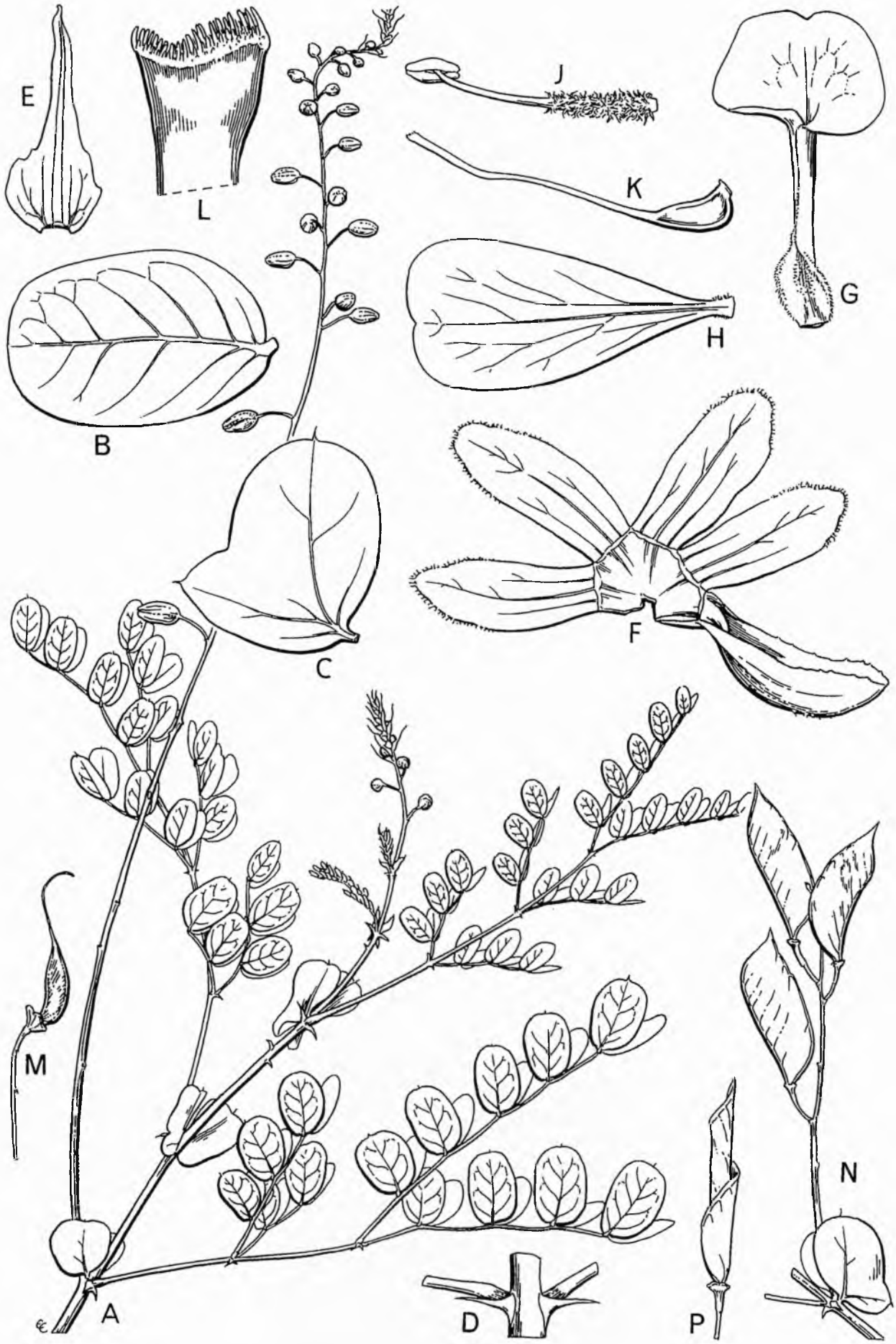


FIG. 70. *Caesalpinia stuckertii*. **A** flowering branchlet x 1; **B** median leaflet undersurface x 3; **C** stipule x 3; **D** detail of foliage prickles x 4½; **E** bract x 7½; **F** calyx opened out x 4½; **G** standard petal x 6; **H** lateral petal x 6; **J** stamen x 4½; **K** gynoecium x 4½; **L** stigma x 36; **M** developing ovary x 1½; **N** fruits x 1; **P** single twisted fruit valve x 1. **C** & **N** from *Venturi* 7697, **M** from *Ruiz et al.* 10488C, **P** from *Aguilar* 241, the rest from *Renvoize et al.* 3538. Drawn by Eleanor Catherine.

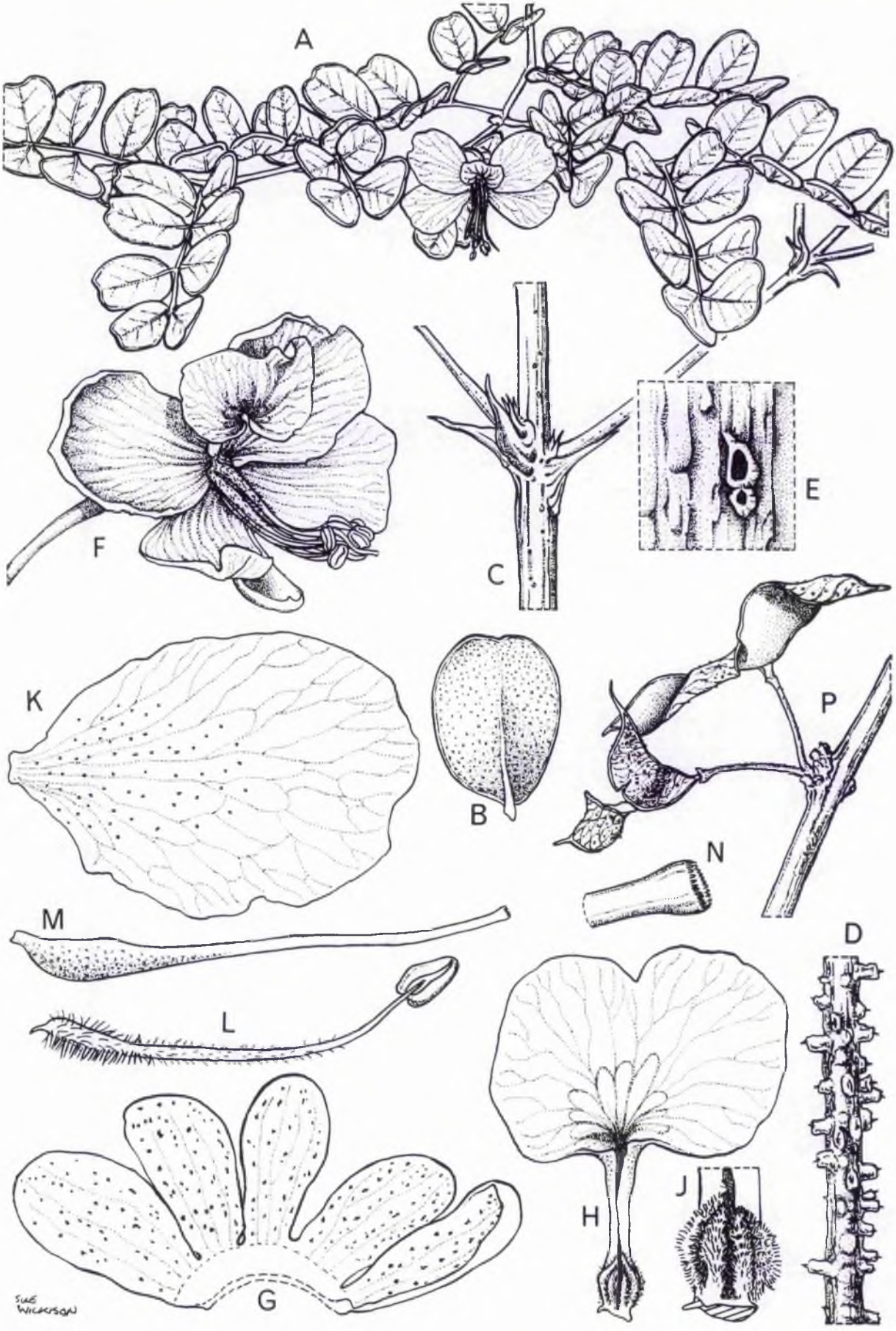


FIG. 71. *Caesalpinia pauciflora*. **A** foliage and flower x 1½; **B** leaflet undersurface x 6; **C** stem with spinescent stipules x 4½; **D** stem bosses with apical prickles x 1½; **E** detail of stem lenticels x 40; **F** flower x 4½; **G** calyx opened out x 6; **H** standard petal x 9; **J** detail of standard petal claw x 18; **K** lower lateral petal x 9; **L** stamen x 9; **M** gynoecium x 9; **N** stigma x 40; **P** dehisced fruits x 1. **A–K & P** from *Lewis* 1854, **L–N** from *Wood & Atchison* 7441. Drawn by Sue Wickison.

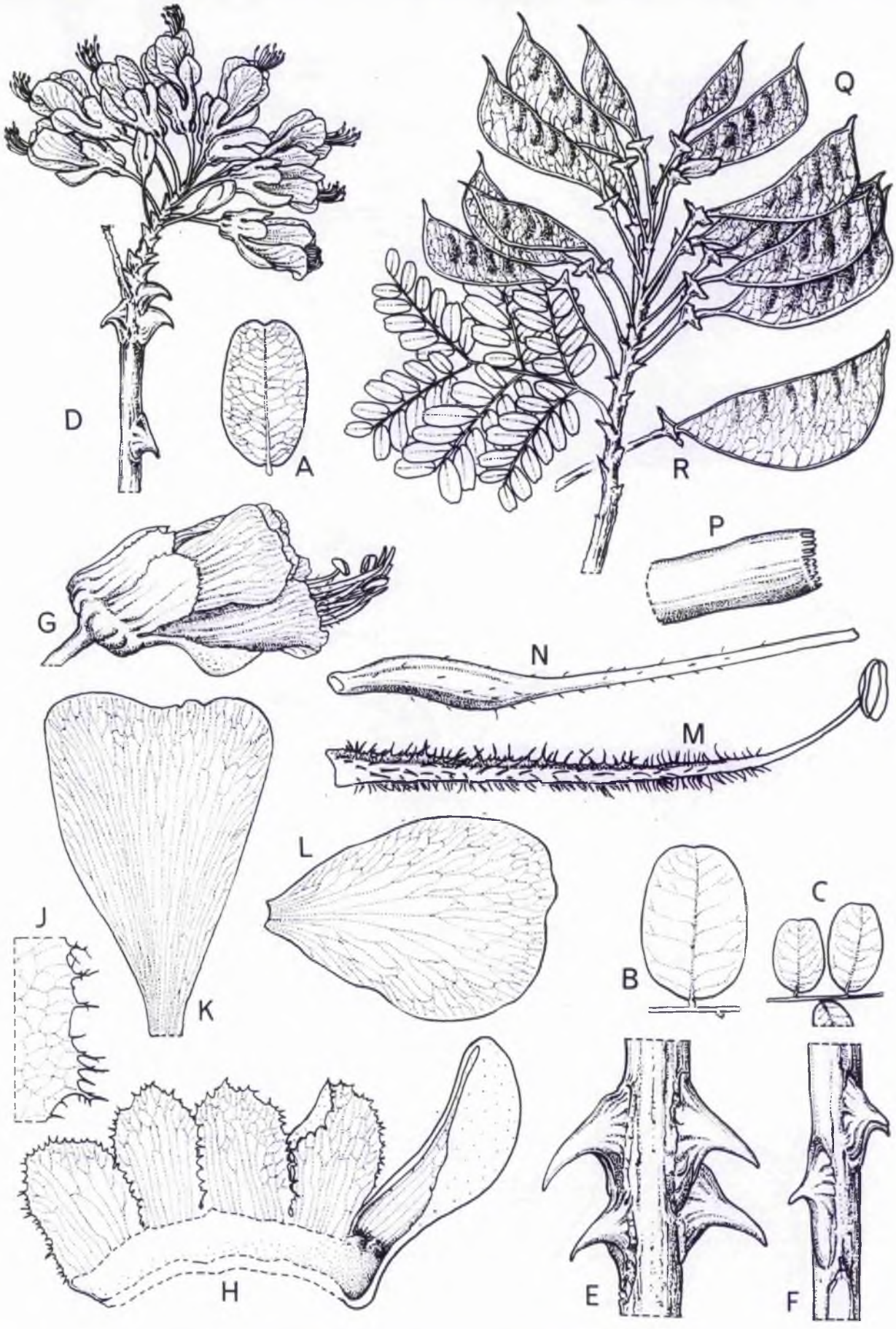


FIG. 72. *Caesalpinia cassioides*. **A** leaflet undersurface x 3; **B** & **C** median leaflets to show size variation x 1; **D** inflorescence x 1; **E** & **F** stem armature x 3; **G** flower side view x 3; **H** calyx opened out x 4½; **J** calyx lobe margin detail x 24; **K** standard petal x 4½; **L** upper lateral petal x 4½; **M** stamen x 6; **N** gynoecium x 6; **P** stigma x 24; **Q** infructescence x 1; **R** immature fruit x 1. **A**, **D**, **E** & **Q** from *Mayolo* 325, **B**, **C** & **R** from *Silverstone-Sopkin* 2004, **G–P** from *Silverstone-Sopkin* 5139. Drawn by Sue Wickison.

FUTURE WORK

i) Fieldwork in Argentina in October 1994 will hopefully provide valuable data on species of *Erythrostemon* not yet seen in the living state.

ii) A cpDNA analysis of *Caesalpinia sens. lat.* is planned in collaboration with Dr S. Harris at Oxford and funds are currently being sought for this.

iii) Data sets on leaflet and floral gland anatomy, seed chemistry, floral ontogeny, wood anatomy, seedling germination and nyctinasty need to be expanded for *Caesalpinia sens. lat.*

iv) Old World taxa of *Caesalpinia sens. lat.* need to be studied in detail.

v) *Caesalpinia sens. strict.* (about 25 species) needs to be thoroughly revised.

vi) Additional information on the reproductive biology of *Caesalpinia calycina* in Brazil is needed to confirm some provisional findings about the apparent sexual lability of the flowers.

vii) A cladistic analysis of each of the infrageneric groups of *Caesalpinia sens. lat.* needs to be carried out at the species level.

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NUMERICAL LIST OF TAXA

1. *Caesalpinia mexicana* A. Gray
2. *C. phyllanthoides* Standley
3. *Poincianella robinsoniana* Britton & Rose
4. *Caesalpinia pannosa* Brandegee
5. *C. nelsonii* (Britton & Rose) J.L. Contr.
6. *C. standleyi* (Britton & Rose) Standley
7. *C. acapulcensis* Standley
8. *C. caladenia* Standley
9. *C. palmeri* S. Wats.
10. *C. exostemma* DC.

10a. subsp. *exostemma*

10b. subsp. *tampicoana* (Britton & Rose) G.P. Lewis

11. *C. hughesii* G.P. Lewis
12. *C. coccinea* G.P. Lewis & J.L. Contr.
13. *C. yucatanensis* Greenman

13a. subsp. *yucatanensis*

13b. subsp. *chiapensis* G.P. Lewis

13c. subsp. *hondurensis* G.P. Lewis

14. *C. nicaraguensis* G.P. Lewis
15. *C. laxa* Benth.
16. *C. hintonii* Sandwith
17. *C. macvaughii* J.L. Contr. & G.P. Lewis
18. *C. epifanioi* J.L. Contr.
19. *C. melanadenia* (Rose) Standley
20. *C. eriostachys* Benth.
21. *C. gaumeri* Greenman
22. *C. pinnata* (Griseb.) C. Wright
23. *C. myabensis* Britton
24. *C. pellucida* Vogel
25. *C. nipensis* Urban

26. *C. glandulosa* Bertero ex DC.
27. *C. marginata* Tul.
28. *C. pyramidalis* Tul.
28a. var. *pyramidalis*
28b. var. *diversifolia* Benth.
29. *C.bracteosa* Tul.
30. *C. gardneriana* Benth.
31. *C. laxiflora* Tul.
32. *C. microphylla* Mart. ex G. Don
33. *C. pluviosa* DC.
33a. var. *pluviosa*
33b. var. *intermedia* G.P. Lewis
33c. var. *peltophoroides* (Benth.) G.P. Lewis
33d. var. *cabraliana* G.P. Lewis
33e. var. *paraensis* (Ducke) G.P. Lewis
33f. var. *sanfranciscana* G.P. Lewis
34. *C. echinata* Lam.
35. *C. calycina* Benth.
36. *C. gilliesii* (Hook.) D. Dietr.
37. *C. fimbriata* Tul.
38. *C. mimosifolia* Griseb.
39. *C. trichocarpa* Griseb.
40. *C. ancashiana* Ulibarri
41. *C. placida* Brandegee
42. *C. exilifolia* Griseb.
43. *C. argentina* Burkart
44. *C. coluteifolia* Griseb.
45. *C. coulterioides* Griseb., emend. Burkart
46. *C. angulata* (Hook. & Arn.) G.P. Lewis
47. *C. caudata* (A. Gray) E.M. Fisher

INDEX TO SPECIES AND SYNONYMS

Accepted names are in **boldface**; synonyms are in *italics*.

APPENDIX 1

FLORAL SECRETORY STRUCTURES IN *CAESALPINIA sensu lato* AND RELATED GENERA

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Abstract. In this preliminary survey of a range of species of the *Caesalpinia s.l.* group, (tribe Caesalpinieae), three types of floral secretory structure are described. These are glandular hairs, secretory idioblasts, and nodular secretory ducts. The systematic and ecological significance of these structures are discussed.

Introduction

Caesalpinia sensu lato is a pantropical genus of some 150-200 species. It includes several distinct informal intrageneric species groupings, each with suites of unique characters; it is likely that at least some of these species groups will eventually be re-established at generic rank. In a preliminary cladistic analysis, Lewis and Schrire (in press) demonstrated that the genus *Caesalpinia*, as presently circumscribed, is polyphyletic, since genera such as *Pterolobium*, *Cenostigma* and *Zuccagnia* are embedded within it. Many species are restricted to certain types of habitat, particularly semi-arid desert. Several types of pollination syndrome are present; different species have bee, humming bird, butterfly, moth and possibly even bat pollinated flowers. Since some or all of these various environmental adaptations may well have occurred more than once, this has resulted in morphological similarities and differences that confuse accurate taxonomic placement of some species, and indicates the need for more detailed examination of certain characters.

It has long been known (eg Dellien 1892; Hemsley and Boodle, 1907; Leelavathi and Ramayya, 1983) that flowers of some species of the *Caesalpinia* alliance have abundant large glandular hairs, of varying distribution. Lewis and Schrire (in press) showed that the development of sepal surface glands is an important character defining the *Haematoxylum* lineage of the *Caesalpinia* group. An initial survey also showed the occasional presence of

subepidermal idioblastic cells, and this prompted a preliminary review of floral secretory structures in the group.

Material and Methods

Since fresh or field-fixed, rather than dried material is necessary for a survey of this kind, this survey was restricted by the availability of suitable material, which consisted of a range of New World species of *Caesalpinia*, together with some samples of related Old World and New World genera (listed together with authorities in Table 1). The *Caesalpinia* species are loosely assigned to several taxonomic groups within the *Caesalpinia* assemblage. Of the taxa available for analysis, *Balsamocarpon*, *Cenostigma*, *Haematoxylum* and *Zuccagnia* probably form part of the ingroup for this survey, *Parkinsonia* is considered basal to *Caesalpinia sl.*, and *Delonix* and *Peltophorum* are among the outgroup taxa (although *Delonix* was not used as an outgroup in Lewis and Schrire, in press).

Living material was fixed in FAA (Formalin Acetic Alcohol) in the field (or in the greenhouse in the case of *C. pulcherrima*), and stored in 70% alcohol. Material was dehydrated through an alcohol series, then taken through an alcohol:Histoclear series to Histoclear, then embedded in Paraplast and serially sectioned using a Reichert rotary microtome. Sections were mounted on microscope slides and stained with safranin and alcian blue, dehydrated through an alcohol series, then taken through Histoclear and mounted in Euparal. Photographs were taken using a Leitz Dialux 20 photomicroscope.

For SEM examination, material was taken through an alcohol series to 100% ethanol, then critical point dried using a Balzers CPD 020, mounted on stubs, coated with platinum using an Emscope SC500 sputter coater, and examined and photographed using a Cambridge 240 SEM or a Hitachi S-2400 SEM.

Table 1: Information on species and material examined, and floral anatomy

taxa	collection details	glandular hairs f=filaments o=ovary p=petals pm=petal margins, s=style	subepidermal idioblasts	secretory ducts	evidence of invertebrate damage (and site)
Caesalpinia s.l.:					
Brasilettia group:					
C. velutina (Britton & Rose) Standley	Lewis et al. 1796, Mexico	pm	+	-	
Caesalpinia s.s. group:					
C. bahamensis Lam.	Lewis 1853, Cuba	-	+	-	sepals
C. pulcherrima (L.) Sw.	Hort.Kew.no.059.78.00564	-	+	-	
Erythrostemon group:					
C. calycina Benth.	Lewis s.n., Brazil	o,(s)	-	-	
Libidibia group A:					
C. coriaria (Jacq.) Willd.	Lewis et al. 1745, El Salvador	f,p	-	-	
Libidibia group B:					
C. sclerocarpa Standley	Lewis et al. 1800, Mexico	f,p	-	-	
Poincianella group A:					
C. standleyi (Britton & Rose) Standley, vel aff.	Rico & Windsor-Shaw 833, Mexico	o,p	-	-	
C. eriostachys Benth.	Lewis et al. 1718, El Salvador	f,o,p,s	-	+	
C. exostemma Benth. subsp. exostemma	Lewis & Hughes 1708, Honduras	o,(pm)	-	-	bud cavity
C. hintonii Sandwith	MacQueen et al. 428, Mexico	p,f	-	-	hypanthium
C. melanadenia (Rose) Standley	Lewis et al. 1792, Mexico	f,o,p,s	-	-	
C. nelsonii (Britton & Rose) J.L. Contr.	Lewis et al. 1794, Mexico	p	-	-	
C. nipensis Urban	Lewis et al. 1814, Cuba	-	+	-	
C. palmeri S.Wats.	Lewis et al 2063, Mexico	o,p,pm	-	-	sepals
C. pannosa Brandegee	Lewis et al. 2033, Baja California	o,(p)	-	-	
C. pannosa Brandegee	Lewis et al. 2044, Baja California	p,s	-	-	filaments
C. placida Brandegee	Lewis et al. 2032, Baja California	o,p,(s)	-	-	
C. yucatanensis Greenman subsp. yucatanensis	Lewis & Hughes, 1759, Guatemala	p	-	-	bud cavity
Poincianella group B:					
C. microphylla Mart. ex G.Don	Taylor et al. 1373, Brazil	f,o,p,s	-	+	
C. pluviosa DC. var. peltophoroides (Benth.) G.P. Lewis, ined.	Lewis 1604, Brazil	f,o,p,s	-	+	
C. pyramidalis Tul. var. pyramidalis	Taylor et al. 1361, Brazil	f,o,p,s	-	+	
C. pluviosa DC. var. sanfranciscana G.P. Lewis, ined.	Lewis & Andrade 1862, Brazil	f,o,p,s	-	+	
Russellodendron group:					
C. vesicaria L.	Lewis et al. 1767, Mexico	-	+	-	
other genera:					
Balsamocarpon brevifolium Clos	Aronson 7721, Chile	o,p,pm,s	-	-	petals
Cenostigma gardnerianum Tul.	Lewis 1342, Brazil	o,(p,s)	-	-	
Cordeauxia edulis Hemsley	Hemming 374, Ethiopia	o		-	
Delonix elata (L.) Gamble	Ellis 110, Ethiopia	-	-	-	
Delonix regia (Boj. ex Hook.) Raf.	Fairchild Tropical Garden, USA, FG63-118A(orig. Africa)	-	-	-	
Haematoxylum brasiletto Karst.	Lewis & Hughes, 1711, Guatemala	-	-	-	hypanthium
Haematoxylum campechianum L.	Hughes 1273, Guatemala	-	-	-	hypanthium
H. dinteri (Harms) Harms	Pearson 4134, S.W. Africa	o,(p,s)	-	-	

Table 1: Information on species and material examined, and floral anatomy

Hoffmannseggia intricata Brandegee	Lewis et al. 2054, Baja California	o,(p,pm)	-	-	bud cavity
Parkinsonia aculeata L.	Lewis s.n., Brazil	-	+	-	petals & filaments
Parkinsonia praecox (= Cercidium praecox (R. & P.) Harms)	Hughes & Lewis 1298, Mexico	-	+	-	
Peltophorum pterocarpum (DC.) K. Heyne	Fairchild Tropical Garden, USA, 77-446 (4-321B)	-	-	-	
Zuccagnia punctata Cav.	Cabrera 30149, Argentina	biserinte (o)	-	-	petals & sepals

Observations and Discussion

1. Trichomes

Most species examined (Table 1) have large capitate glandular hairs on various parts of the surface, sometimes widespread over petals, filaments and ovary, but more often localised in particular regions, such as the petal claws (in e.g. *C. nelsonii*), or the petal margins and tips (Fig. 22), or the surface of the ovary (e.g. *C. calycina*, *C. exostemma*, *C. pannosa*, *Cenostigma gardnerianum* and *Cordeauxia edulis*). These glandular trichomes are formed mainly by division and enlargement of epidermal cells, although subepidermal tissue also contributes to some extent. They may be long- or short-stalked or even sessile, and the glandular heads vary in morphology from rounded (Figs. 7, 9) to club-shaped (Figs. 1, 6, 8, 22), the latter type sometimes with a terminal depression that collects the secretion product. Both of these shapes may occur on the same flower (Figs. 8, 9), although club-shaped ones are more commonly present in some species (e.g. *C. hintonii*, *C. palmeri*, *C. pannosa*) and rounded ones in others (e.g. *C. placida*, *Hoffmannseggia intricata*). Club-shaped hairs in particular often have a row of enlarged, secretory epidermal cells in the apical depression (Fig. 22). In some species, such as *Balsamocarpon brevifolium*, the glandular hairs are often very long-stalked. In *Cordeauxia edulis* several glandular hairs were observed with a hollow centre to the head, probably as a result of cell breakdown. Tucker et al., 1984, reported hollow 'inflated', probably secretory trichomes in *Bauhinia*, and discussed their significance. In most species non-glandular trichomes (mostly uniseriate) are also present, often with contents (Fig. 12), and sometimes associated with glandular trichomes. In *C. pluviosa* var. *peltophoroides* for example, long-stalked capitate glandular trichomes with non-glandular branches from the stalks are present at the petal margins (Fig. 3), these are also present in *C. exostemma*, although with less obviously glandular heads (Fig. 13). In *Zuccagnia punctata* the ovary is covered with unusual long biseriate trichomes (Fig. 14), which may or may not be glandular. These biseriate hairs form an acropetal progression along the ovary; with large multiseriate swollen bases at the base of the ovary to entirely biseriate hairs at the tip. In *Cenostigma gardnerianum*, stellate trichomes, many with one or two glandular branches (Figs. 5, 10), occur around the outer part of the hypanthium and on the ovary, these may be indicative of the close developmental relationship between non-glandular and glandular types of trichome. Indeed, on the ovary there is a gradual acropetal progression from largely non-glandular

stellate hairs at the base, through ones with occasional glandular branches, to mainly entirely glandular hairs at the ovary tip. Furthermore, some species of *Caesalpinia s.l.*(often individuals within one population) have ovaries that are either densely glandular or densely hairy, or even glabrous and eglandular, or transitional types between these extremes. Glandular hairs are absent from occasional species of *Caesalpinia* and most species of *Haematoxylum* and *Delonix* examined (Table 1), although in *Delonix elata* groups of long protruding stomata are often present at the bases of petals (Fig. 27), apparently not associated with secretory tissue.

2. Subepidermal idioblasts

A few species (*C. velutina*, *C. bahamensis*, *C. vesicaria*, *C. pulcherrima*, *C. nipensis*) have enlarged isolated subepidermal secretory cells (idioblasts) embedded in often dark-staining tissue in the petals and/or sepals (Figs. 25, 26), and in some cases in the filaments and ovary; these are sometimes visible in herbarium material as sunken white dots. These cells are relatively numerous in *C. bahamensis* (Fig. 25) and *C. pulcherrima* (especially in the unopened flower bud), but less frequent in *C. nipensis*, *C. vesicaria* and *C. velutina*. *C. velutina* (Fig. 26) is unusual in having both frequent glandular trichomes and subepidermal idioblasts. In *Parkinsonia aculeata* and *P.(Cercidium) praecox* enlarged idioblastic cells are present in the hypanthium,either subepidermally, or 2-3 cell layers beneath the epidermis (Figs. 15-17). They are often so numerous in this region as to comprise a hypodermal tissue, rather than individual idioblastic cells, particularly in *P. aculeata*, where they are smaller than in *P.(Cercidium) praecox*. In *Peltophorum pterocarpum*, unusual enlarged idioblastic cells are present in the petals (Fig. 23), apparently mucilage-filled, and occasionally with intrusively elongated branches between neighbouring cells. The homology of these structures is not clear, and requires further examination.

The presence of secretory idioblasts has apparently not previously been recorded in Caesalpinioideae flowers. However, Lersten and Curtis (1993) described subepidermal idioblasts in leaves of *Caesalpinia pulcherrima* and *Parkinsonia aculeata*, and reviewed the occurrence of these cells in leaves of Caesalpinioideae in general, citing in particular the work of Dellien (1892), which recorded them in leaves of several species of several tribes

of the subfamily. They speculated that the idioblasts may have some anti-herbivoral function.

3. Secretory ducts

A third type of secretory structure occurs in some closely related species of *Poincianella* groups A and B (Table 1), *C. eriostachys*, *C. microphylla*, *C. pluviosa* var. *peltophoroides* and *C. pyramidalis*. These species always have mucilage-filled secretory ducts at intervals in the sepals, petals (Fig. 29), and in a swollen region of the anther tip (Fig. 28), and also in swollen nodules around the pedicel (Fig. 30). These discrete regions of secretory tissue are oval or sometimes elongated in cross section (often kidney-shaped in the anther tip: Fig. 28), dense, usually red- (or sometimes blue and red) staining (with safranin and alcian blue). The surrounding parenchyma cells are somewhat flattened into a sheath. Dellien (1892) recorded similar secretory regions with a distinct epithelium in the leaves of species of Bentham & Hooker's section '*Caesalpinaria*' (equivalent to *Poincianella B* in this survey, and including *C. microphylla* and *C. pyramidalis*), often causing black dots on the leaves. These secretory 'nodules' closely resemble mucilage-filled nodules formed by bacterial symbionts in leaves of a few other families, particularly Rubiaceae (Miller, 1990), but the presence of bacteria has not been demonstrated in our material, and these structures are currently the subject of further investigation.

Systematic and ecological considerations

The flower, and particularly the closed flower bud (Figs. 21, 25), is clearly a complex environment with much variation between taxa. With the exception of *C. velutina*, which is unique in having both floral glandular hairs and (sparse) secretory idioblasts, among the species of *Caesalpinia sensu lato* with secretory idioblasts, floral glandular hairs are absent (Table 1), suggesting that they share a similar role. The presence of invertebrate parts inside many of the buds (Table 1), either embedded within the petal tissue (Figs. 18-20) or in the central bud cavity (Fig. 24), often with an accompanying fungal invasion, demonstrates that many species are subject to herbivore attack. Although there are exceptions to this, such invasion is generally more common in cases where glands are sparse or absent (Table 1), indicating that the secretory structures may have a role against predation; little is known, however, about the chemistry of their secretion products. For example, both New World species of *Haematoxylum*, which lack glandular hairs, had

extensive invertebrate damage in the hypanthium and particularly at the base of the sepal junction. In contrast, the Old World species *H. dinteri*, with glands, showed no sign of attack by parasites or herbivores. The floral regions with the densest concentrations of such structures are also indicative of a defensive function. Several species (Table 1) have copious glandular trichomes on the ovary; presumably a region that requires greater defence investment from the plant since it contains the potential future generation and also holds food storage products that are attractive to herbivores or parasites. Another region that is apparently vulnerable to attack is the hypanthium, where possible herbivoral structures were observed in several species. This region is the main site of concentration of subepidermal idioblasts in *Parkinsonia* spp.

Secretory idioblasts, which are absent from flowers of the outgroup taxa, may well represent an apomorphy for some of the ingroup taxa. They apparently link the basal groups *Caesalpinia s.s.*, *Brasilettia* and *Parkinsonia* (Table 1) (although in the latter they are largely restricted to the hypanthium), together with *C. nipensis* (*Poincianella*) and *C. vesicaria* (Russellodendron). Interestingly, the biochemical data also links *C. vesicaria* with *Brasilettia* (Kite and Lewis, in press) and morphological data suggest that *C. nipensis* should be transferred to *Caesalpinia s.s.* From Lewis and Schrire (in press) secretory idioblasts are apparently present in the basal members of the ingroup, and were later lost; however, more data are required to test this hypothesis. The mucilage cells of *Peltophorum pterocarpum* also require further investigation to establish their homology.

Floral glandular hairs are absent from the outgroup taxa *Delonix* and *Peltophorum*, and also from the possibly basal taxa *Parkinsonia* and *Caesalpinia s.s.* (although present in *Brasilettia*, also possibly basal). However, they represent a characteristic feature of most of the rest of the ingroup, with some exceptions, such as *Haematoxylum* (where they are recorded only in the taxonomically isolated species *H. dinteri*), and possibly *Zuccagnia*, although the ovary hairs in the latter may well be derived from a glandular type. *Cenostigma* and *Caesalpinia eriostachys* (currently considered a distinct element within *Poincianella A*), which are probably closely related, share a similar type of stellate hair that is transitional with glandular types (Figs. 5, 10). This character would certainly benefit from a more detailed survey, since variations in gland morphology and distribution may well define particular species groups. For example, pyriform glandular hairs are

characteristic of some species of the *Pomaria* group (Lewis and Schrire, in press), for which no fixed material was available for this investigation.

Nodular secretory ducts are characteristic of a small group of species, mainly from the Brazilian north-east (with the exception of *C. eriostachys*, from Mexico and Central America). These species form a distinct grouping within the *Poincianella* assemblage, linking *C. eriostachys* (*Poincianella A*) with the species of *Poincianella B*.

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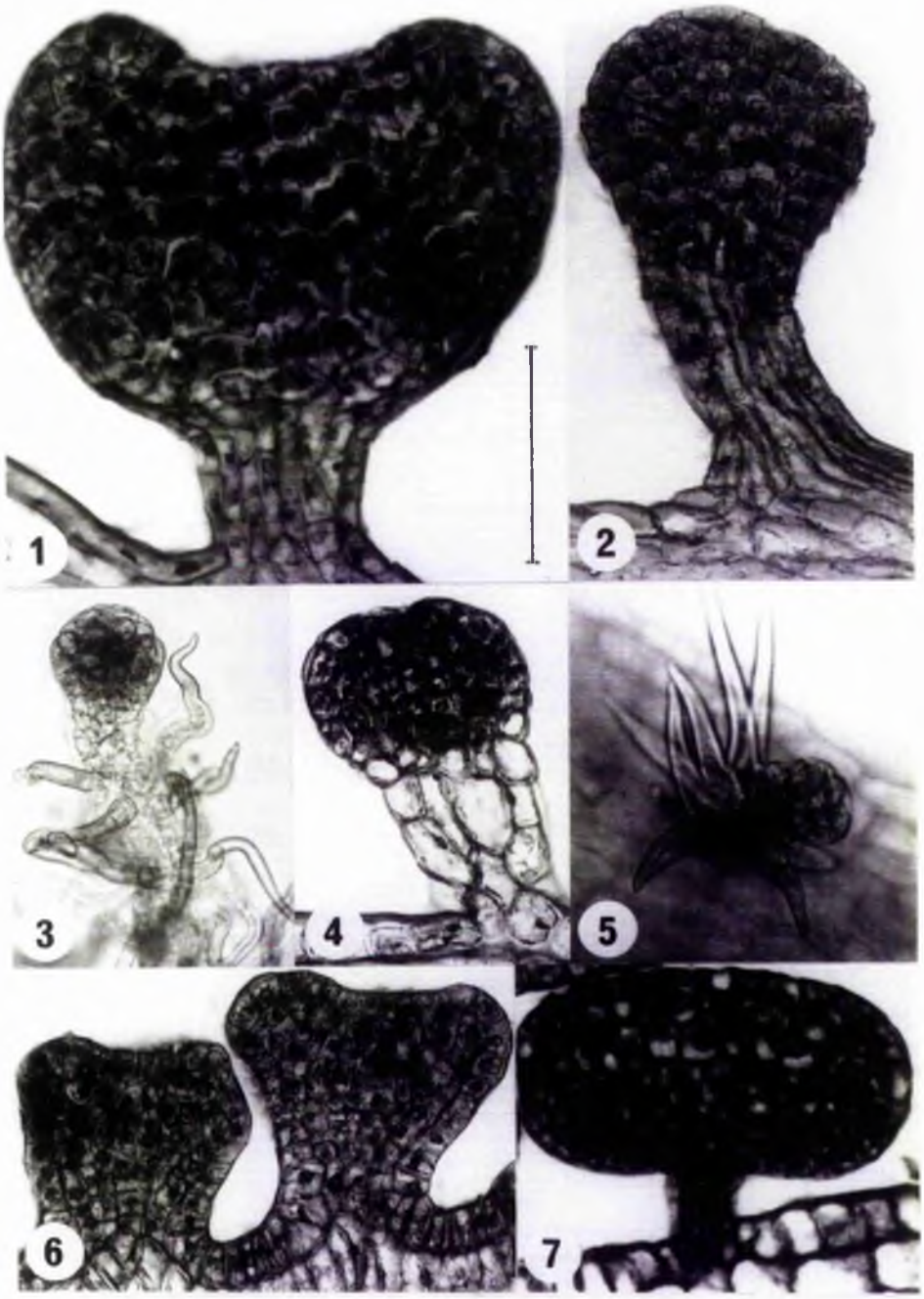
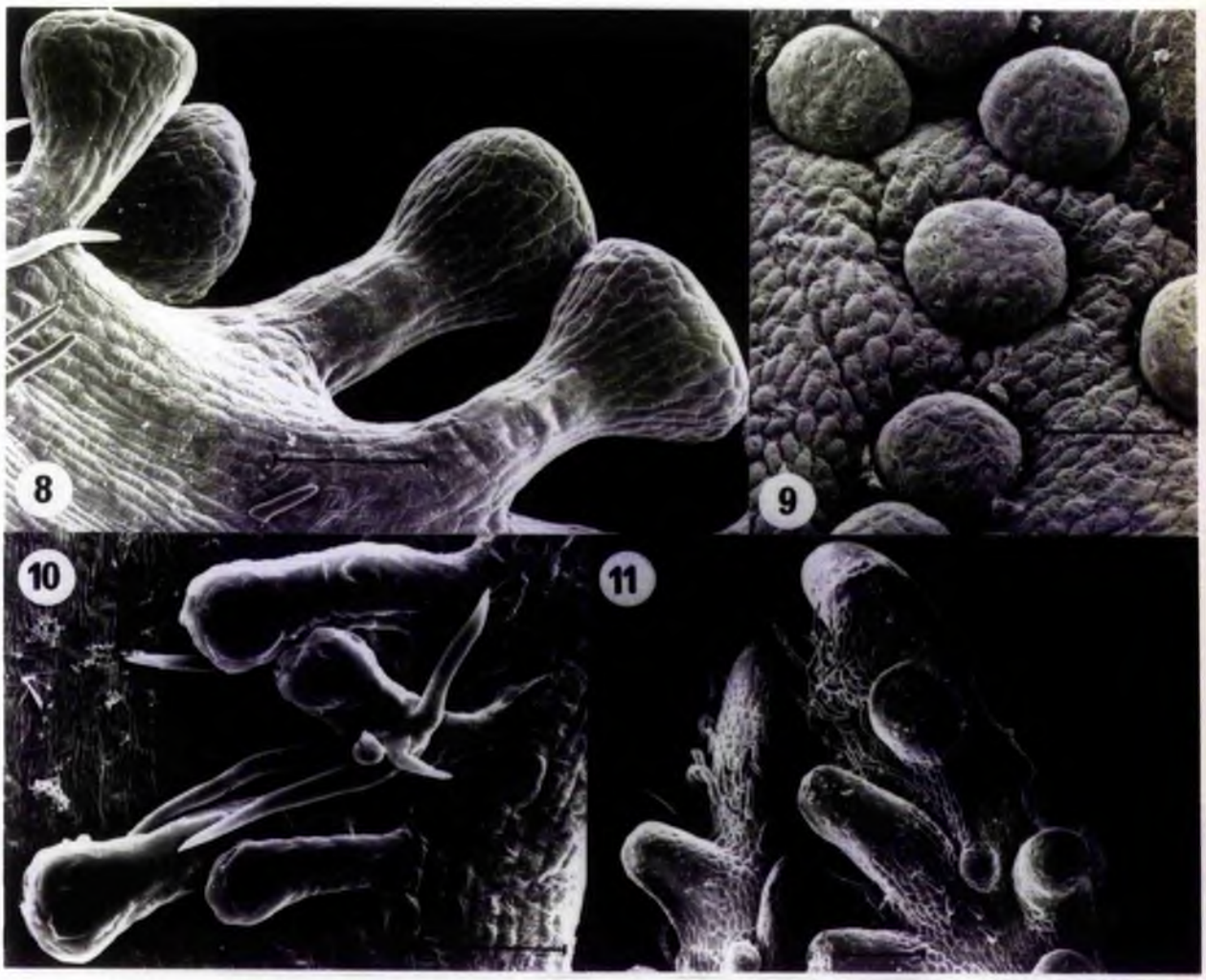
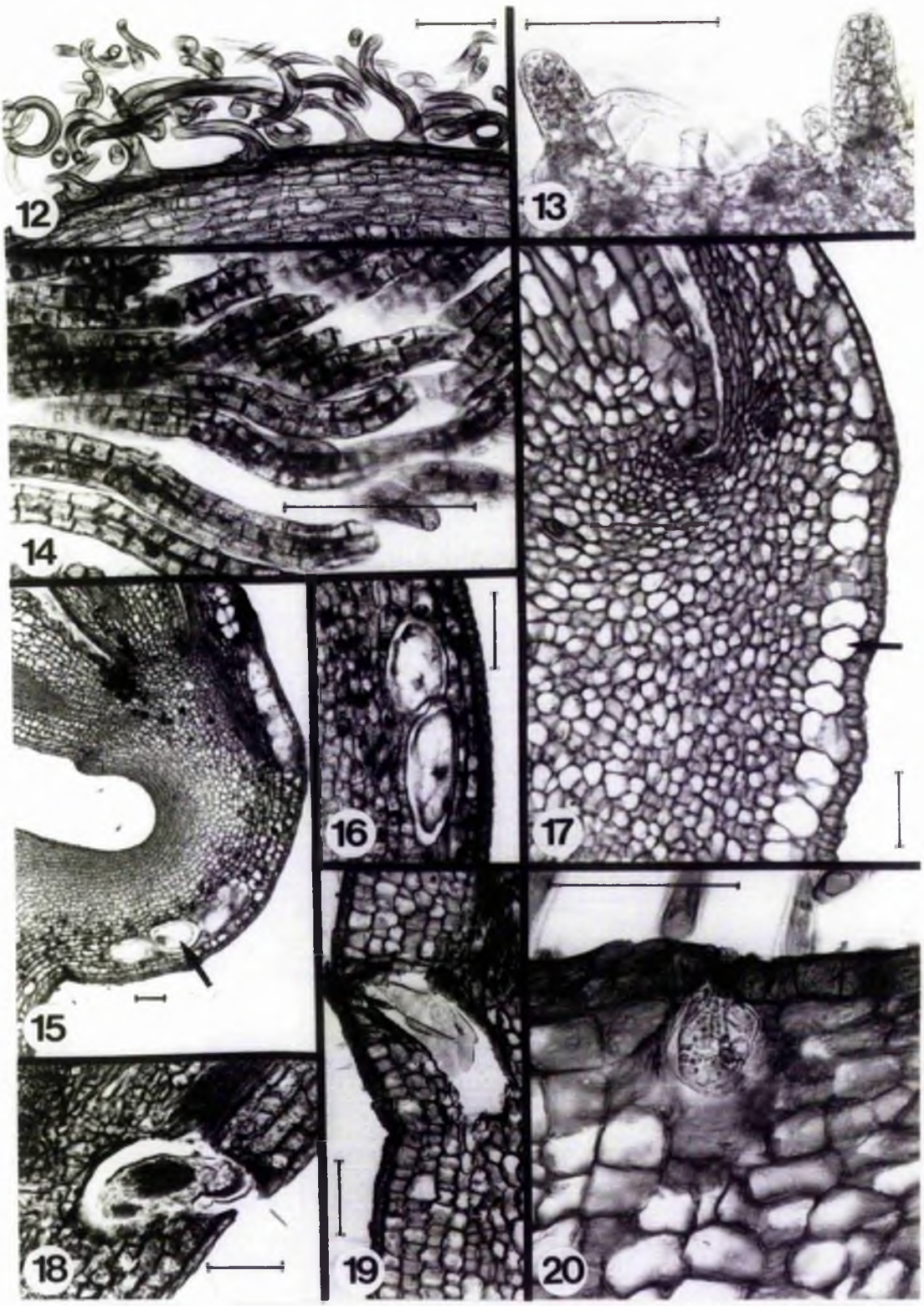


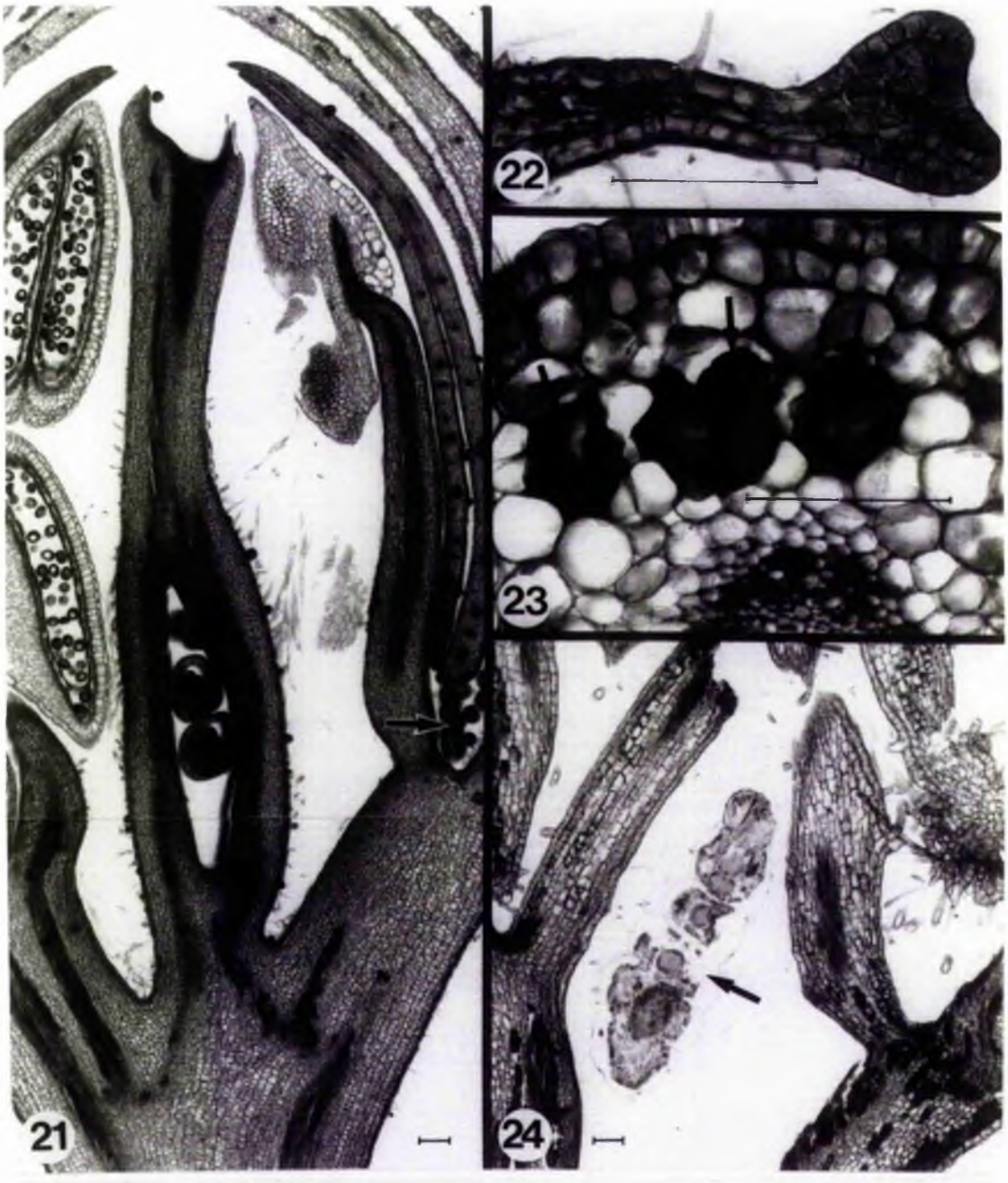
Figures 1-7. Sections of glandular hairs. Fig. 1. *Caesalpinia hintonii*, club-shaped petal hair with terminal depression. Fig. 2. *Caesalpinia placida*, long-stalked hair on ovary. Fig. 3. *Caesalpinia pluviosa* var. *peltophoroides*, hair at petal margin with non-glandular branches on stalk. Fig. 4. *Caesalpinia pyramidalis*, hair with stalk cells larger than head cells. Fig. 5. *Cenostigma gardnerianum*, stellate hair on sepal with glandular branch and several non-glandular branches. Fig. 6. *Caesalpinia pannosa*, short-stalked club-shaped hairs on ovary. Fig. 7. *Caesalpinia yucatanensis* subsp. *yucatanensis*, hair with rounded head and short narrow stalk, on dorsal surface of petal. Scale bar = 100μm (Figs. 2-7 as for Fig. 1).



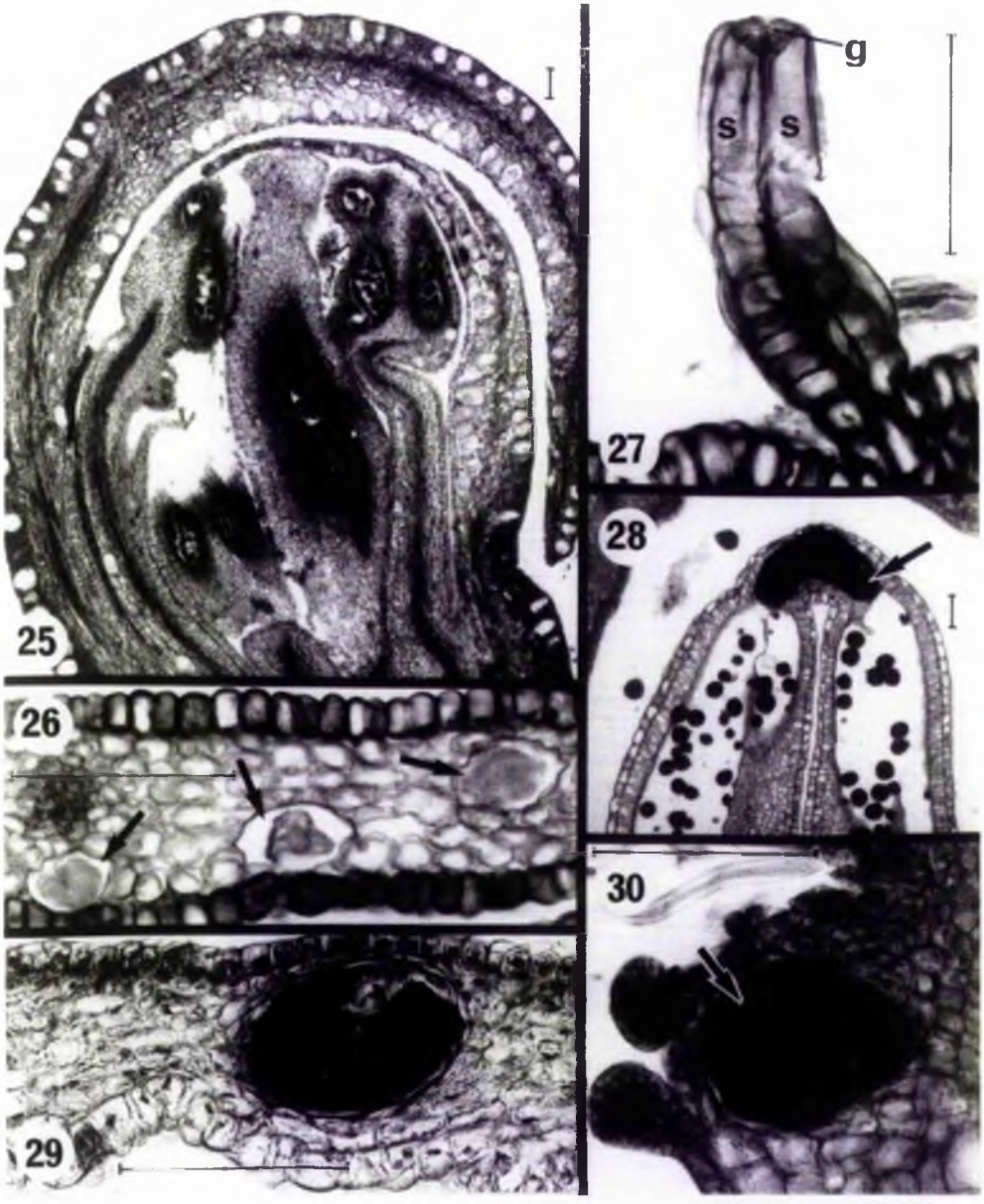
Figures 8-11. Glandular hairs, SEM. Fig. 8. *Caesalpinia nelsonii*, long-stalked club-shaped hairs. Fig. 9. *Caesalpinia nelsonii*, sessile glands on dorsal surface of petal. Fig. 10. *Cenostigma gardnerianum*, glandular hairs on sepal, one with several non-glandular branches. Fig. 11. *Caesalpinia velutina*, glandular hairs at tips of calyx lobes. Scale bar = 100μm.



Figures 12-20. Fig. 12. *Caesalpinia hintonii*, curled uniseriate non-glandular hairs with contents, on ovary. Fig. 13. *Caesalpinia exostemma* subsp. *exostemma*, hairs at petal margin, with ill-defined heads and non-glandular branches from stalk. Fig. 14. *Zuccagnia punctata*, long biseriate hairs on ovary. Figs. 15, 16. *Parkinsonia* (*Cercidium*) *praecox*, idioblasts (arrowed) in hypanthium. Fig. 17. *Parkinsonia aculeata*, idioblasts (arrowed) in hypanthium. Fig. 18. *Haematoxylum brasiletto*, invertebrate damage in hypanthium. Fig. 19. *Caesalpinia hintonii*, invertebrate damage in hypanthium. Fig. 20. *Parkinsonia aculeata*, invertebrate damage in petal. Scale bar = 100μm.



Figures 21-24. Fig. 21. *Caesalpinia standleyi* vel. sp. aff., LS flower bud just before anthesis. Few glandular hairs on ovary and petal 'claw' (arrowed). Fig. 22. *Caesalpinia calycina*, glandular hair at petal tip. Elongated secretory epidermal cells in cup-shaped region of gland. Fig. 23. *Peltophorum pterocarpum*, mucilage cells in cross section of petal base. Fig. 24. *Hoffmannseggia intricata*, invertebrate (arrowed) in bud cavity. Scale bars = 100μm.



Figures 25-30. Fig. 25. *Caesalpinia bahamensis*, LS very young closed flower bud, with copious secretory idioblasts in petals and sepals. Fig. 26. *Caesalpinia velutina*, enlarged secretory idioblasts (arrowed) in petal. Fig. 27. *Delonix elata*, protruding stoma at petal base, with elongated subsidiary cells (s) supporting guard cells (g). Fig. 28. *Caesalpinia pyramidalis*, LS anther tip, showing swollen region with mucilage-filled kidney-shaped cavity (arrowed). Fig. 29. *Caesalpinia pyramidalis*, mucilage-filled cavity in petal, with ring of cells visible. Fig. 30. *Caesalpinia pluviosa* var. *peltophoroides*, mucilage-filled secretory cavity in nodule on pedicel, with two glandular hairs on surface. Scale bars = 100μm.

APPENDIX 2

Sexual Systems in two species of *Caesalpinia* (Caesalpinioideae - Leguminosae) from Bahia, Brazil

Summary: The sexual systems of *Caesalpinia calycina* Benth. and *C. pluviosa* DC. var. *sanfranciscana* G.P. Lewis, ined. were studied from early March to the end of April 1991 in Bahia, Brazil. Both species are apparently self-incompatible. *C. calycina* is pollinated by at least three species of carpenter bees and *C. pluviosa* var. *sanfranciscana*, with smaller flowers, has a wider range of pollinators including some *Centris* species. In *C. calycina* there appears to be a direct relationship between the "trap-lining" bees, flower presentation, fruit set per inflorescence and the initiation of an andromonoecious floral syndrome in middle and upper flowers of an inflorescence.

Introduction

Caesalpinia, as currently circumscribed in most Floras, is a pantropical genus of some 150-200 species although of the 25 generic names currently in synonymy under *Caesalpinia* at least 9 might be resurrected to generic rank in due course leaving about 25 species in *Caesalpinia sensu stricto*. Few species of *Caesalpinia sensu lato* have been studied with regard to their reproductive biology, notable exceptions being *Caesalpinia* (*Poincianella*) *eriostachys* (Bawa & Webb, 1984, Bullock, 1985), and *C. pulcherrima* (Cruden and Hermann-Parker, 1979, Bullock, 1985). In addition to these two, Bullock (1985) also studied *C.* (*Libidibia*) *coriaria*, *C.* (*Libidibia*) *sclerocarpa*, *C.* (*Poincianella*) *caladenia* and *C.* (*Brasilettia*) *platyloba* in Mexico and showed that all six are andromonoecious. Recently, Cocucci et al. (1992) have published a detailed study of the floral biology and pollination by crepuscular sphingid moths in *C.* (*Erythrostemon*) *gilliesii*. Dioecy occurs in *C.* (*Guilandina*) *bonduc* and allies (Polhill & Vidal, 1981) and *C.* (*Brasilettia*) *velutina* and allies (Contreras, pers. comm. 1989). The floral syndromes appear to be closely related to type of pollinator. Vogel (1990) illustrated (his Fig. 11) four of the flower types encountered in *Caesalpinia sens. lat.* each of which has a different pollinator — bee, butterfly, moth and humming bird.

Caesalpinia calycina is restricted to caatinga vegetation of south central Bahia with the exception of one known collection from Pernambuco (Heringer *et al.* 765). Several of its morphological characteristics suggest relationships with *C. gilliesii* from Chile and Argentina and *C. fimbriata* from Bolivia, both in the *Erythrostemon* group. *C. pluviosa* var. *sanfranciscana* is endemic to central Bahia and northern Minas Gerais but field observations suggest that it hybridises with *C. laxiflora*. *C. pluviosa* var. *sanfranciscana* falls within Bentham & Hooker's section *Caesalpinaria* which is the South American equivalent to Britton and Rose's genus *Poincianella*.

Experiment location and methodology

For logistical reasons a field site within one days driving distance of the Cocoa Research Institute, Itabuna, Bahia was chosen. *Caesalpinia* species in Bahia were mapped from herbarium specimens and valuable phenological data was gleaned in the process. The small town of Livramento do Brumado (13° 43'S, 41° 51'W) was selected as a base from which to work on two species of *Caesalpinia* growing as easily accessible components of open caatinga vegetation. Three experimental sites were set up, 10, 20 and 35 km south of Livramento do Brumado along the road to Brumado. At Sites 1 (10 km) and 2 (20 km) *C. calycina* populations were easily accessible from the main road and at Site 3 (35 km) a small population of *C. pluviosa* var. *sanfranciscana* bordered either side of a dry riacho.

Most experimental work was undertaken on *C. calycina* but for both species in this study various tagging and controlled pollination experiments were set up to study flower production, pollination systems and fruit set.

The average number of inflorescences per shrub, flowers per inflorescence and their opening sequence were determined. For *C. calycina* an estimate of the number of open flowers per day within a population was made. The anthesis period, flower presentation, longevity, stigma type, sequence of anther dehiscence and post pollination changes in flower morphology and colour were observed for both species. Nectar volume and solute concentration of the nectar were estimated at intervals for *C. calycina* using micropipettes and a pocket refractometer.

Controlled pollinations were performed in the field between 08.00 and 13.00 h in order to establish the breeding system. Flowers were enclosed in white muslin bags the day

before anthesis and emasculations needed for some of the tests were made at that time. Seventeen shrubs of *C. calycina* and three trees of *C. pluviosa* var. *sanfranciscana* were used in such experiments. Cross-pollinations of previously emasculated flowers used mixed pollen of at least two donor plants 50 to 100 metres distant. Self-pollinations were made with unemasculated flowers using their own pollen. Automatic self-pollination was tested by simple bagging. A random sample of 100 flowers were tagged in order to establish natural fruit set (control). Pollinations were considered to have been effective when flowers persisted beyond the usual abscission period (48 to 72 hours in *C. calycina*) and the fruits started to grow. A subsample of hand cross- and self-pollinated pistils were fixed in FAA at intervals of 18, 24, 48 and 72 h for subsequent studies of pollen tube growth using aniline blue stain and flourescent microscopy (Martin, 1959).

The average number of fruits per infructescence and seeds per fruit were counted for both species. In *C. calycina* it became apparent, as hand pollinations were attempted, that some flowers did not present a normally developed pistil. To investigate this aspect further, flowers from various positions along the inflorescence were dissected to study the stamen vs. pistil condition. In addition, a random sample of 100 infructescences were scored for fruit-set position along the rhachis. This latter census was facilitated by the fact that in *C. calycina* the woody pedicels of fruits are persistent, even after the valves have fallen away, whereas abscised flowers fall with the pedicel attached, leaving a scar on the rhachis. Because of this difference, the same sample of infructescences could also be used to estimate fruit/flower ratios. In a further survey, the ovule number per developing fruit, and final seed number and position in mature fruits were assessed.

Flower visitor behaviour was observed and examples of the range of visitors were caught and identified. Pollinators and opportunists were determined and flower visiting behaviour of both was recorded on 35 mm colour transparencies.

Results

Caesalpinia calycina Benth.

i) Flower presentation and phenology

Evidence from herbarium specimens and observations by de Carvalho (pers. comm., 1990) suggest that *C. calycina* usually reaches its peak flowering period (when over half the population is in flower) in January to early February. Occasional late rains can,

however, trigger the species into a secondary flowering as witnessed by the massive flowering following five days of almost continual rain at Livramento do Brumado in early March 1991. Following the late rains, new inflorescences opened their basal flowers and older inflorescences opened new flowers higher up the rhachis. Where no fruit had set on the lower portion of the rhachis this now acted as an extended peduncle.

There was a difference in the length of this second flowering peak between sites 1 and 2, apparently controlled by the height of the terrain above the water table. Flowering at site 1, on higher ground, was over before plants at site two, on lower ground, had reached peak flowering. At site 1, a population of approximately 100 shrubs reached maximum flower presentation two weeks after the end of the rains. The shrubs were scattered over an area of about 300 x 300 m with the closest shrubs touching but others between ten and fifty metres apart.

On average, a 2.5 m tall shrub supported ten inflorescences, which are held erect above the foliage (Fig. 1). Mean flower number per rhachis was 30 (range 8-85, N = 100), and each inflorescence opened an average of two (1-3) flowers each day. The population at site 1 thus presented approximately 2000 open flowers each day at peak flowering.

Flowers open at dawn (05.30 h in March) and remain open for one day. Irrespective of whether successful pollination has occurred the petals shrivel and change colour from yellow to orange-pink by the following morning, and flowers which have been unsuccessfully pollinated abscise within 48-72 h after opening.

Fresh anthers vary somewhat in colour from creamish pink to deep salmon pink or orange-pink. With age these become dark red. Pollen is not available immediately at anthesis and the ten anthers dehisce sequentially over a period of about six hours, the top three first and the upper seven well before the lower three. Pollen is presented as individual grains in slightly sticky clumps but there are no viscin threads as in *C. pulcherrima* which is butterfly pollinated (Cruden & Hermann-Parker, 1979). As the bud opens the stigma is displayed as a bright green structure surrounded by a ring of pink anthers and at first appears to be receptive to pollen. On closer observation (i.e. with a 10 x hand lens) some, but not all, stigmas at this stage are not "open". As is common in many *Caesalpinia* species the chambered stigma (Owens, 1990) has a terminal pore surrounded by a ring of unicellular, papilla-like cells. At the base of each of these cells is

FIG. 1. *Caesalpinia calycina*, inflorescences held erect above the foliage.

FIG. 2. *Caesalpinia calycina*, perforated plate (arrowed) at base of papilla-like cells fringing stigma chamber.

FIG. 3. *Caesalpinia calycina*, open hermaphrodite flower showing stamen and style positions.

FIG. 4. *Xylocopa grisescens*, with pollen on abdomen, visiting flower of *Caesalpinia calycina*.

a perforated plate (Fig. 2). At flower anthesis the papilla-like cells sometimes appear to close off the stigmatic pore but they soon become turgid and erect thus opening the stigmatic chamber. It seems probable that the basal perforated plates facilitate uptake of water from adjacent style cells causing turgor in the cells that fringe the stigma chamber which thus reflex at or just before anthesis (further observation is needed to be sure of the timing of this event). The turgid cells around the rim of the stigma chamber then act collectively as a circular comb assisting in the removal of pollen from visiting bees.

In fully open flowers of *C. calycina* the stamens are held downwards with the style apex slightly curved upwards away from them (Fig. 3) but after the stigma has received a pollen load the style curls downwards and inwards, or sideways and outwards, thus removing the stigma from contact with subsequent pollinator visits.

On the dorsal face of the standard petal and on the petal claws, short-stalked, mushroom-shaped, glandular hairs are present, often in large numbers. These glands vary in colour from yellow to orange. They are easily detached and often break off when nectar is sampled with a micropipette.

ii) **Pollinators, Flower Visitors and Nectar**

The number and species of flower visitors varies depending on weather conditions, time of day and availability of other food sources (pollen and nectar). Flower visitors to *C. calycina* seek nectar and none actively collect pollen.

Pollinator observations commenced in early March 1991 when most of the caatinga legumes and indeed most other species in the area were flowerless, but some shrubs of *C. calycina* were still producing flowers on a few inflorescences.

Only large solitary bees, principally *Xylocopa grisescens* (Fig. 4) and *X. frontalis* (Fig. 6), but also *X. cearensis* and a new species of *Epicharis* (Fig. 5) (C. O'Toole, pers. comm., 1992) are of the correct size and morphology to effect pollination. Rows of stiff hairs on the underside of the bee's abdomen act as efficient pollen combs. The force with which the bee lands on a flower of *C. calycina*, together with the way it inwardly curves its abdomen (presumably as a balancing movement to stabilize the bee while drinking nectar), ensures that pollen is forced into the stigmatic chamber. It is worth noting that hand pollinations proved to be tricky because of the small size of the stigma, the flexibility of the long style and the force required to place pollen in the stigmatic chamber. An

individual *Xylocopa* often returns to the same flower of *C. calycina* every thirty minutes or so. Nectar volumes and concentrations are at their highest between about 10.00 and 15.00 h and open flowers constantly replenish their nectar — at midday up to 10 µl are produced per flower every 30 minutes. The length of time that an individual bee remains on one flower varies but is usually about 3 seconds.

Three species of *Centris*, *C. tarsata*, *C. pectoralis* and *C. fuscata*, regularly visited the flowers of *C. calycina* for nectar but were too small to effect pollination and were never observed touching anthers or stigma. Many other opportunist visitors rarely or never visited this species once rain had stimulated flowering in other species. Notably, a species of emerald humming bird (probably *Chlorostilbon aureoventris pucherani*), a regular visitor before the rain, hardly paid any attention to *C. calycina* after the rain. Being yellow and not tubular the flowers of *C. calycina* cannot be called typical humming bird flowers and the bird was never seen touching anthers or stigma with any part of its body. It placed its beak down the thickened groove of the "standard" claw in order to reach the nectar and while doing so hovered in front of the flower with its body well away from petals and sexual parts. Another opportunist visitor before the rain was a small metallic-green bee, a species of *Euglossa*, which collected nectar by forcing its tongue between the lateral petals and stamen filaments.

A small number of nectar samplings were carried out on *Caesalpinia calycina* but results from this limited survey do not present any clear patterns. Individual flowers, on inflorescences covered in plastic bags, accumulated between 6 and 20 µl of nectar per hour in their calyx tubes. On any one inflorescence an average of two flowers will be open on any one day so that it is not possible to compare nectar production in lower, hermaphrodite, and upper, functionally male, flowers on the same inflorescence at the same time. Comparison of hermaphrodite flowers on one inflorescence with 'male' flowers of another showed no significant difference in nectar production. Nectar was found to have a mean volume of 14.9 µl (N = 11) and mean solute concentration of 23.5% (range 19-30).

Interestingly, when many inflorescences were covered by muslin bags in order to carry out hand pollination experiments the *Xylocopa* species still attempted to gain access to the covered flowers. The bees trap-line shrub and inflorescence position until in very close proximity to the flower when further visual and perhaps olfactory cues help the bee to

FIG. 5. *Epicharis* sp. nov. collecting nectar from flower of *Caesalpinia calycina*.

FIG. 6. *Xylocopa frontalis* (pollinator) and *Apis mellifera* (nectar robber) visiting flowers of *Caesalpinia calycina*.

FIG. 7. *Epicharis* sp. nov. with *Senna* pollen on thorax.

FIG. 8. *Xylocopa grisescens* probing unopened bud of *Caesalpinia calycina* at 05.30 h.

orientate itself so as to land in such a way that its head is immediately placed within the concave standard petal. In very windy conditions the Xylocopas still land with remarkable accuracy although just occasionally their abdomen does not immediately make contact with anthers and/or stigma. Smaller opportunist bees often land in different positions to the *Xylocopa* species and several species seem to have adopted various strategies for robbing nectar. (Fig. 6)

Species of *Xylocopa* (Fig. 4) and *Epicharis* sp. nov. (Fig. 5) pick up large quantities of pollen while drinking nectar. The pollen accumulates on the undersurface of the bee's abdomen and is ideally positioned to be deposited on a receptive stigma of another open flower. Given that few flowers per shrub are open at any one time (a maximum of 20 on a plant with 10 inflorescences) pollen carry over to flowers of another shrub is greatly enhanced. The length of time of pollen viability is, however, unknown. No other visiting insects or birds were observed to transfer pollen between flowers. The *Xylocopa* species do visit other legumes in the local vicinity, but pollen placement is partitioned on different parts of the bees body. *Xylocopa grisescens* and *Epicharis* sp. nov., for example, also visit species of *Senna* (Caesalpinioideae - Cassiinae). During my two months in the field several species of *Senna* came into flower for short periods of one to two weeks and *X. grisescens* invariably frequented these between visits to *Caesalpinia calycina*. Prominent amongst the *Senna* species flowering in March 1991 was *S. aversiflora* (Lewis & Andrade collection number 1934). All of these *Senna* species (which have dry, nectarless, flowers) are visited for pollen by the large bees which effect buzz-pollination. Pollen is mostly deposited on the back of the bees thorax (Fig. 7).

Bee activity varied depending, amongst other things, upon the weather, but there were usually peaks of activity at midday and between 15.00 and 16.00 hours. Often, in mid-afternoon it appeared that *Xylocopa* species would ward off attempted flower visits by males of *Eulaema nigrita* (Apidae) but further work is needed to confirm this.

iii) **Pollination system**

Flowers start to open at 05.30 h. (first light, March—April 1991) and species of *Xylocopa* start to visit the flowers from this time, even facilitating flower opening in some cases. *Xylocopa grisescens*, for example, was observed probing buds on the point of anthesis (before the anthers had started liberating pollen) and was evidently trying to reach

potential nectar (Fig. 8). Flowers had no detectable scent. The bees appeared to be quite selective as to which flowers they visited early in the morning, sometimes preferring the almost closed buds to fully open flowers and occasionally visiting faded flowers from the previous day.

Flowers typically have bright yellow petals, c. 1.5-2 cm long, and the "standard" petal is distinctly concave for the lower two thirds of its inner face. Into this concavity the head of a visiting *Xylocopa* fits perfectly as it forces its way to the nectar. The "standard" rarely has small flecks of orange on its inner face but these are never as striking as those observed in several other species of *Caesalpinia*. During the twelve hours that the flowers are open the four lateral petals, which vary somewhat in shape between flowers, become damaged and torn as the large, bulky bees use them as landing platforms and footholds; this especially applies to the lower two laterals. At first the five sepals are held forward and support the petals but the four lateral ones reflex a few hours after anthesis. The 10 stamens (2.2—2.4 cm long) and the pistil are held forward and downwards, more or less at right angles to the standard petal.

Stigma receptivity is crucial to pollen germination and the timing of this is both limited and uncertain. What is apparent is that pollen has to be placed into the stigma with some force. The chamber can accommodate many times more pollen grains than are needed to fertilize the 4 to 6 ovules in the ovary but pollen grains probably need to touch the chamber wall before germination can take place so that a large pollen mass should enhance the chances of fertilization. However, it is likely that effective pollination is not simply pollinator or pollen-load restricted but that the pollen also needs to be forced into the stigmatic chamber at the correct time of day and that a liquid droplet is necessary in the stigma.

Several genera in the Caesalpinioideae require a liquid droplet in the stigmatic chamber to assist in pollen capture and to stimulate germination (Owens, 1990). The timing of pollen deposition in the stigmatic chamber may be critical if pollen tube growth is to be stimulated. It is not yet clear if the stigma is receptive before or after the first anthers of the same flower have dehisced. Owens (1990) studied the morphology of stigmas in 24 species of 11 genera in the *Peltophorum*, *Caesalpinia* and *Dimorphandra* groups of tribe Caesalpinieae (the sample included 11 species of *Caesalpinia sens. lat.*). In all species where fresh open flowers were examined the stigmatic chamber was filled by a droplet of

clear stigmatic fluid. 'The timing of fluid appearance and its duration appeared variable with respect to individual flowers, prevailing environmental conditions, stigma receptivity and species'.

As a flower opens the style curls upwards as it expands and the stigma is thus presented chamber-up. A visiting *Xylocopa* or *Epicharis* grasps the lateral petals, and sometimes the back of the sepals also, with its legs and forces its head into the 'standard' concavity pushing the standard upwards thus opening a gap to the staminal fenestrae and so to the nectar. (Fig. 9) While doing this, pollen is scraped from its abdomen by the stigma fringe cells and is forced into the stigma chamber by the weight of the bee as it curls its abdomen around and under the stamens and stigma. Shortly after the stigma has received a pollen load the style bends either downwards or sideways so that bees contact only the anthers, although there are occasional exceptions. It is possible that after pollen deposition in the stigma chamber the style may actually lengthen slightly but this has to be confirmed.

iv) **Sexual System**

Flowers tend to decrease in size very slightly towards the inflorescence apex. Random sampling of open flowers in different positions on different inflorescences revealed the presence of two types of flower: hermaphrodite, with a fully developed pistil, and functionally male with a very reduced pistil. Some intermediate type flowers with partially developed pistils were also encountered. The male flowers produce a similar quantity of pollen and nectar as the hermaphrodite flowers. The hermaphrodite flowers with long styles are lowermost on an inflorescence and the male flowers are uppermost but the relative proportions of each vary. Although less obvious, hermaphrodite vs. male flowers could also be distinguished in dissected buds. Although male flowers were only found in the upper inflorescence, they were not consistently present in all inflorescences. Rather, the occurrence of male flowers was correlated with fruiting success in the lower rhachis, and it was possible to predict the sexuality of the upper flowers on this basis. Thus, where fruits were set in the lower third or so of the inflorescence, the upper flowers would be male, whereas lack of fruit-set in the lower rhachis was correlated with hermaphrodite flowers (buds) in the upper third of the inflorescence. This situation was also reflected in the sample of 100 infructescences which were analysed for fruit position. In this sample,

FIG. 9. *Xylocopa grisescens* seeking nectar at open flower of *Caesalpinia calycina*.

FIG. 11. *Caesalpinia calycina* fruits opened to monitor seed-set and ovule abortion.

FIG. 14. *Caesalpinia pluviosa* var. *sanfranciscana*, paniculate inflorescence.

FIG. 15. *Trigona* sp. robbing pollen of *Caesalpinia pluviosa* var. *sanfranciscana*.

23% of infructescences had some fruits in the upper third of the rhachis, and the presence of such fruits was, in general, negatively correlated with fruit-set in the lower third.

Laboratory analyses of fixed pistils reveal that there does not appear to be any inhibition of self-pollen germination in the stigma. Although only 29% of stigmas with self-pollen in them showed any pollen tube growth this contrasted with an even lower figure of 18% for stigmas with cross-pollen. The penetration of ovules by pollen tubes in samples analysed was 5.9% (possibly as high as 8.9%) for hand-selfs versus 13.1% for hand-crosses. It is clear, therefore, that pollen tubes from some self-pollen grains are capable of reaching the micropyle of an ovule. It is, however, not known whether some self-pollen tubes are inhibited somewhere along the length of the style. In both self- and cross-pollinations some ovules had been penetrated 18 hours after pollen was placed in the stigma chamber

v) **Fruit-set and Seed-set**

In any one population of *C. calycina* some shrubs are more successful than others in the numbers of fruit that they produce per infructescence. Fruits develop quickly in size, ovule expansion occurs, and the seeds then slowly build up food reserves. Unripe seeds are yellow; mature seeds are dark brown. Occasionally, some shrubs have mature seeds which are yellow with pale brown speckling, but seed colour is consistent for any one shrub. Fruits are explosively dehiscent and usually open with a loud cracking noise, with both valves tearing away from the lignified pedicel which remains as a persistent peg.

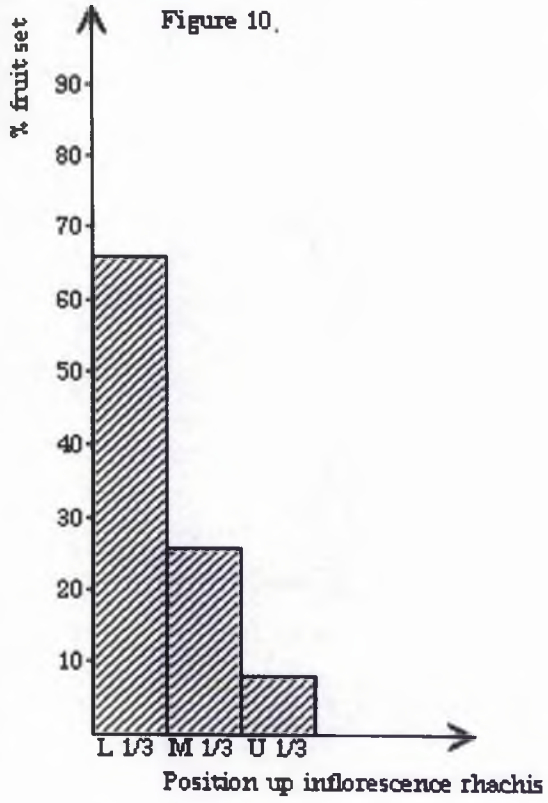
On a sample of 100 infructescences, 8% produced no fruits; 59% produced 1-4 fruits; 23%, 5-8 fruits, and 10%, 9-12 fruits. From a total of 3083 flower positions (indicated by pedicel scars and persistent pedicels) on a second sample of 100 infructescences, 393 produced mature fruit, a natural fruiting success of 12.75%.

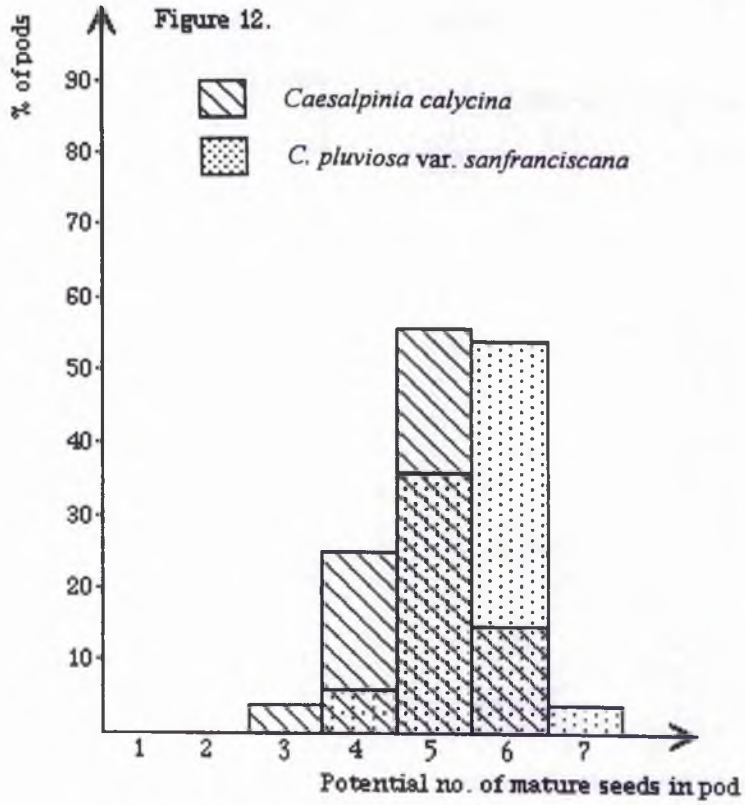
In a third sample, one hundred infructescences were selected arbitrarily to assess the number and position of fruits resulting from each inflorescence. What was immediately apparent was that far more fruits were set in the lower third than in the upper two thirds. This, however, should be balanced against the fact that not all inflorescences support or have the potential to produce the same number of flowers. So, for fruit-set assessment, each infructescence, was divided into lower, middle and upper thirds (e.g. a 24-flowered inflorescence had the potential to produce 8 fruits in each third).

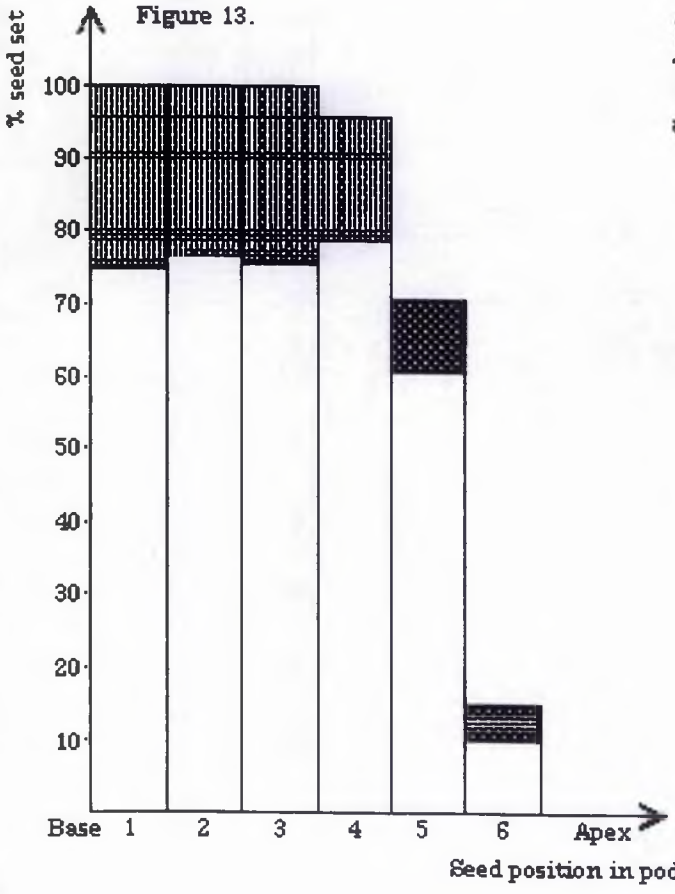
In this third sample, which included 5% that set no fruit at all, 411 mature fruits were counted. Of these 271 (66%) were in the basal third, 107 (26%) in the middle third and only 33 (8%) in the upper third (see Fig. 10). In addition to the 5 infructescences with no fruit set, 17 more set no fruit in their basal third; of these 17, thirteen did produce fruit in the middle third and 3 of these went on to produce fruit in the upper third as well. Four infructescences that produced no fruit in the basal third went on to produce one or two fruits in the upper third only. Out of the 100 infructescences sampled, 23 produced some fruit (max. 3) in the upper third.

Flowers in the upper third of an inflorescence often have much reduced, non-functional pistils so that they are functionally male. It appears that the more fruits that set in the basal third of an inflorescence, the more likely it is that middle third and especially upper third flowers will suppress pistil development. This helps to explain the strong bias towards much greater fruit production in the lower third. Once lower flowers have set fruit, it is presumed that less nutrients are available to higher flowers so that a switch to maleness in upper flowers is energetically sound. Flowers in the upper third, irrespective of whether they are hermaphrodite or male, continue to produce nectar as well as pollen and this ensures that the trap-lining bees constantly transfer cross-pollen between plants. If, however, lower flowers do not set fruit it is more likely that middle and upper flowers will retain their bisexuality and thus continue to be capable of fruit production. Young fruits remain green until the seeds begin to fill out and ripen, so they can photosynthesize and manufacture sugars without relying totally on food from the leaves.

As a control, 100 flowers were tagged arbitrarily to assess natural fruit set. While most of the flowers tagged were basal, hermaphrodite ones, the random sample will have included some female-sterile flowers so that the percentage fruiting success recorded should not be taken as a maximum. After 5 days 33% of the flowers had retained ovaries and persisted on the inflorescence, the others abscising. After a further 9 days just over one quarter of the developing ovaries had fallen, to give a 25% initial fruiting success 2 weeks after tagging. It is likely that this percentage fruiting success would drop even further due to juvenile fruit abscision as suggested by the 12.75% fruiting success recorded on the 3083 flower positions discussed earlier, but fruit development after 2 weeks was not monitored.







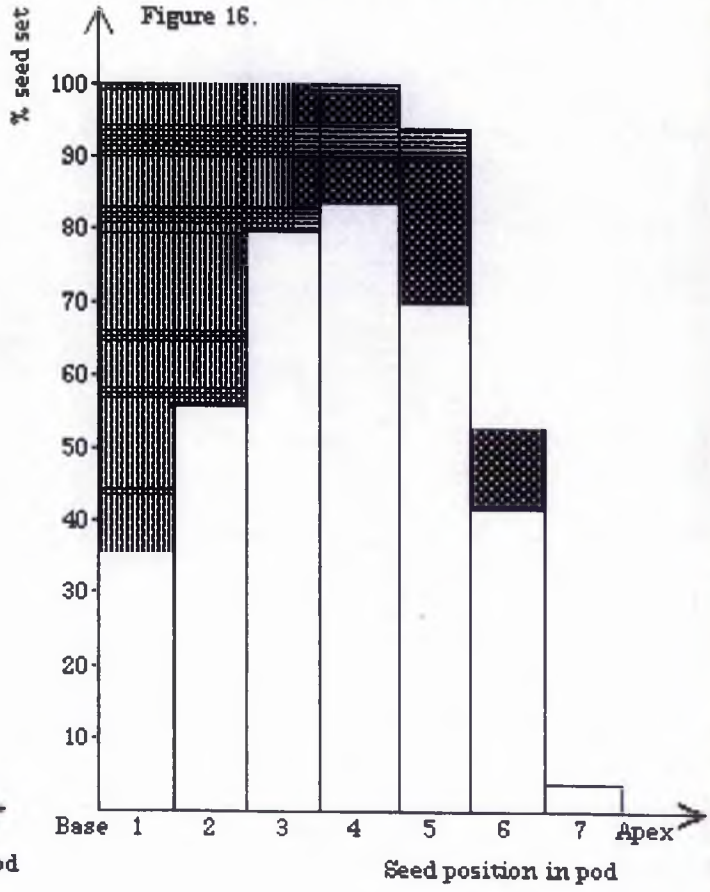


FIG. 10. Fruit-set position in *Caesalpinia calycina.*

FIG. 12. Seed-set potential in *Caesalpinia calycina* and *C. pluviosa* var. *sanfranciscana.*

FIG. 13. Seed-set/ovule abortion in fruits of *Caesalpinia calycina.*

FIG. 16. Seed-set/ovule abortion in fruits of *Caesalpinia pluviosa* var. *sanfranciscana.*

= ovule abortion

100 developing fruits were randomly selected to assess potential seed number per fruit, ovule abortion, and seed-set (Fig. 11). The average number of potential seeds (i.e. ovule positions) per fruit was 4.8 (range 3—6). Of the 100 fruits sampled, four had 3 ovule positions, 25 had 4 ovule positions, 56 5 ovule positions and 15 6 ovule positions. (Fig. 12). Seed-set was scored for each position from base to apex of each of the 100 pods. (Fig. 13). 75% of the ovules in position one (i.e. closest to the pedicel) set seed, 78% in position 2 and 76% in position 3. A proportion of the fruits did not have ovules in positions 4, 5 and 6 but of those that did 82% set seed in position 4, 86% in position 5 and 66% in position 6.

No hand self-pollinations resulted in fruit-set and most "selfs" abscised from the inflorescence within 24 to 48 hours after pollen placement. 20% of hand-crosses left on shrubs resulted in fruit-set. This compared with a 25% natural fruiting success (as assessed from persisting young fruits) two weeks after random tagging of 100 flowers. It can be assumed that most, if not all, of these fruits resulted from natural cross-pollinations even though the source of the pollen was unknown.

Although no fruits were set as a result of hand self-pollinations, some ovules were penetrated by pollen tubes so it seems possible that a late-acting self-incompatibility system might be operating.

***Caesalpinia pluviosa* DC. var. *sanfranciscana* G.P. Lewis, ined.**

i) Flower Presentation and Phenology

Caesalpinia pluviosa var. *sanfranciscana* at experimental site 3, 35 km S of Livramento do Brumado, formed a small population of well over 30 individuals on both sides of the road bordering a dry river bed, and is common along the road between 20 to 35 km S of Livramento do Brumado. *C. pluviosa* var. *sanfranciscana* falls into a different group of species to *C. calycina* and presents a different habit, being usually a medium-sized, multiple-trunked tree to about 6 m. in height. At the study site some trees were in full flower, some in fruit only and some sterile; some fertile trees had recognisably distinct flowering and fruiting branches. As for *C. calycina*, flowering was pulsed by recent rains but the overall flowering period was shorter, being almost over within three weeks. After rain each inflorescence rhachis grew, on average, 2 cm. Flowers are displayed in leafy panicles and individual trees produce very many more flowers than those of *C. calycina*.

Pedicels increase greatly in length just before anthesis and there are two zones of disarticulation, one just below the calyx, and one at the point of attachment to the inflorescence rhachis. If flowers abort they first disarticulate at the calyx base, and the pedicel abscises later.

In the late afternoon some flowers start to gape slightly at the apex in preparation for full opening the next day. At this stage the style is curved, the stigma is evident within the sepal and petal opening, and the anthers are pink and turgid. The stigmatic pore is very small (less than 0.5 mm in diameter) and while the bud is just beginning to open, the stigma is bright green and appears apparently receptive, but the stigmatic fringe cells are bent inwards to cover the stigma opening so that it cannot receive pollen. Flowers open in the early morning and start to wilt by mid to late afternoon; they are 12 hour flowers as with *C. calycina*. At anthesis the stigma faces upwards and outwards but later the style curves and the stigma faces downwards. By the time the cells that fringe the stigma chamber are turgid and erect the anthers have started to dehisce in sequence, with the upper three dehiscing first.

A sample 6 m tree was used to assess the total number of potential flowers presented to pollinators through time, the number of flowers open on any one day, and the possible fruit-set. Flowers are aggregated into racemes, then compounded into panicles (Fig. 14), and finally into larger leafy panicles. The total number of panicles on the sample tree was 497, the total number of racemes 3164. The average number of flowers per raceme was about 30 (range 20—50), so that the total possible number of flowers through the flowering period for one tree was 94,920. The average number of flowers open per raceme on the sample tree was 1.04 (range 0-3) but it should be noted that the sample was made at 15.00 h and during a day there is normally heavy flower drop. It is estimated that if the measurement had been made at 09.00 h the number of open flowers could be increased by 10—20%. Nevertheless, the number of open flowers available to nectar seekers at 15.00 h on the sample tree of *C. pluviosa* var. *sanfranciscana* was at least 3,290.

ii) **Pollinators and Flower Visitors**

The majority of the visitors seek nectar but some insects, notably species of *Trigona*, appear to rob pollen, i.e. they eat, rather than collect it and do not effect pollination. (Fig.

15). These bees remove pollen from both dehisced anthers and from the stigma chamber. Larger bees, such as *Xylocopa grisescens* and *X. frontalis*, pick up pollen on the underside of the middle and lower part of their abdomen while visiting the flowers to collect nectar. Species of *Centris* also visit the flowers and certainly come into contact with both anthers and stigmas. A species of humming bird (unidentified) visits the upper flowers of larger panicles held above the crown, and thus away from the foliage, but the bird's body does not come into contact with anthers or stigma. The *Xylocopa* species usually visit more than one open flower per leafy panicle and more than one panicle per tree before moving on, thus much self pollen is probably delivered to stigmas. The Xylocopas seem to prefer the higher inflorescences in brighter sunlight but this could be because these were further away from me! Just as for *Caesalpinia calycina*, *Xylocopa* species visiting *C. pluviosa* var. *sanfranciscana* also visit species of *Senna* to collect pollen by buzz-pollination.

iii) **Sexual System**

The majority of flowers used in hand self-and cross-pollinations and left for fruit development were destroyed by a plague of caterpillars. From another subsample of hand pollinated flowers, pistils were fixed in FPA, 24 and 48 hours after pollinations. All of these stigmas, from both self- and cross-pollinations, contained germinating pollen but only 2 out of 13 ovules (crosses), and 2 out of 24 (selfs), examined had been penetrated by pollen tubes. This hardly constitutes a sample from which conclusions can be made but does show that, as for *C. calycina*, pollen tube growth is not inhibited in the stigma.

Most hand pollinations dropped within 72 hours of pollen placement and no hand selfs or crosses went on to set fruit, although due to caterpillar damage to gynoecia the sample of undamaged ovaries was very small. Zero fruit set from hand cross-pollinations is, however, little different from the 4% fruit set obtained from a random tagging of 100 flowers (see below).

iv) **Fruit- and Seed-Set**

A tree completely in fruit was analysed for total fruit- and seed-set. Each panicle produced an average of 3 fruits (range 0—9) and each raceme an average 1.2 fruits (range 0—5). Extrapolating to the sample flowering tree, 497 panicles could potentially produce a total of c. 1,491 fruits.

A random 50 pods were sampled to look at seed-set. These yielded 186 mature seeds from 284 ovules so that the average number of mature seeds per fruit was 3.72 (range 1—6). Thus, an average 6 m tree could potentially yield c. 5,546 ripe seeds. The potential number of ovules for the sample tree was 94,920 (i.e. the total flower positions available through time) multiplied by 5.68 (the average number of ovules per ovary, range 4—7), a total of 539,145. We can conclude that about 1% of the potential ovules actually develop into ripe seeds. A certain percentage of the apparently available ovules are, however, not produced or are rendered redundant. As in *C. calycina*, not all the flowers on a tree of *C. pluviosa* var. *sanfranciscana* are functionally hermaphrodite and, although the percentage of male flowers is not known, this reduces the number of potential ovules. The relationship between fruit-set and the switch to maleness in upper flowers of an inflorescence needs to be further investigated in this taxon. Insect damage to flowers and developing young fruits causes abortion of these organs thus further reducing the number of ovules that can mature into seeds. In addition, there is a large natural flower drop during the day presumed to be partly a result of unsuccessful pollinations.

A total of 100 flowers on four trees were tagged to look at natural fruit-set. After 5 days, 16% of the flowers had enlarging pistils, the other 84% had dropped. After a further 10 days three quarters of the fruits had aborted to leave only a 4% fruit-set from the original 100 flowers. Some young fruits had aborted due to insect damage. Random observation revealed that several medium to full-sized fruits resulting from a previous flowering had dried and shrivelled but continued to persist on the trees. Their maturation to fully ripe pods was almost certainly prohibited by lack of available resources during a particularly dry season.

Of a random sample of 100 fruits, 6 had 4 ovule positions, 36 had 5 ovule positions, 54 6 ovule positions and 4 7 ovule positions. (Fig. 12). As for *C. calycina* seed-set was scored for each ovule position from base to apex of each pod. In constrast to *C. calycina*, but similar to Bawa and Webb's (1984) findings for *C. eriostachys*, there is a much higher percentage of ovule abortion in the two most basal positions than in positions 3, 4 and 5. Only 36% of ovules in position 1 and 56% in position 2 set seed compared with 80%, 84% and 75% in positions 3, 4 and 5 respectively. (Fig. 16). Only 1.08% of seeds or developing ovules were insect damaged.

Discussion

1) Pollination biology

Melittophily is the most common pollination syndrome in *Caesalpinia sens. lat.* species although butterfly pollination has been described in *C. pulcherrima* by Cruden & Hermann-Parker (1979) and nocturnal sphingid pollination has been reported in *C. gilliesii* by Cocucci, Galetto & Sersic (1992).

C. calycina and *C. pluviosa* var. *sanfranciscana* are both well adapted to bee pollination and the larger flowers of *C. calycina* are closely associated with large carpenter bees of the genus *Xylocopa*. These bees are "trap-liners" (Janzen, 1971) and visit the same shrubs, inflorescences and flowers regularly throughout the day. The anthers of each flower open sequentially ensuring that each flower presents some pollen at intervals during the day, thus maximising pollen transfer and mixing. Some of the bees visiting partially opened and/or faded flowers of *C. calycina* early in the day are probably experimenting with the species for the first time, i.e. they are commencing a learning curve. Alternatively, their trap-lining type memory presumably allows them to arrive at an individual plant or inflorescence and then other floral cues come into operation. Perhaps limited exposure of a bright green stigma within a ring of pink-red anthers acts as an early visual cue to the pollinator. Certainly, bees do not visit completely closed buds. There may also be some olfactory cue but the flowers had no detectable scent. The exact function of the mushroom-shaped glands on the standard petal are not known though pollinator attraction and/or mechanical protection are likely functions. They may serve as tactile cues to nectary position or as mechanical protection against opportunist nectar robbers. In other species of *Caesalpinia* similar pixie-cup-shaped glands are secretory and antifungal or antiherbivore activity cannot be excluded until more is known about their secretory products.

2) Breeding System

Self-incompatibility (SI) has been reported in various Caesalpinioideae, e.g. *Bauhinia benthamiana* [= *B. ungulata*] (Bawa & Webb, 1984), *Caesalpinia* (*Poincianella*) *eriostachys* (Bawa, 1974; Bullock, 1985), *Caesalpinia* (*Libidibia*) *coriaria* and *C.* (*Libidibia*) *sclerocarpa* (Bullock, 1985), and *Senna bicapsularis* (Bawa & Buckley, 1989) whilst *Senna pallida* was reported as self-compatible in the latter study, as were

Caesalpinia (*Poincianella*) *caladenia* and *C. pulcherrima* by Bullock (1985). SI of the "late-acting" type (Seavey & Bawa, 1986), that is to say, with self-pollen tubes reaching the ovules as observed in *C. calycina* and *C. pluviosa* var. *sanfranciscana*, was also reported for *C. eriostachys* by Bawa & Webb (1984), who also observed that all selfed flowers were abscised by 72 hours. This phenomenon obviously requires further study.

Andromonoecy was reported as being relatively uncommon in Caesalpinioideae by Arroyo (1981), with a scattering of examples listed for the genera *Gleditsia*, *Dialium*, *Bauhinia*, *Apuleia* and *Arcoa*, and one species in *Caesalpinia*, *C. pulcherrima*. Bullock (1985), however, noted that pistil size varied in all five *Caesalpinia* species, *viz. C. caladenia*, *C. coriaria*, *C. eriostachys*, *C. pulcherrima* and *C. sclerocarpa*, included in his study of breeding systems in a Mexican tropical deciduous forest community, and it is possible that andromoneocy is more widespread in Caesalpinioideae than hitherto detected. This hypothesis is also supported by Simpson and Neff (unpublished data) who have found andromonoecy in *Caesalpinia* (*Erythrostemon*) *exilifolia* and *Caesalpinia* (? *Hoffmannseggia*) *pumilio* (pers. comm., 1990). Low ratios of fruits to flowers per inflorescence are common and suggestive of andromonoecy (Bullock, 1985).

In *Caesalpinia pulcherrima* (Cruden & Hermann-Parker, 1979) and the five species of *Caesalpinia* in Bullock's (1985) survey, the presence of male staminate flowers has been regarded as a fixed aspect of the breeding system, although the number of male flowers within an inflorescence may be variable.

In *Bauhinia pauletia*, Heithaus *et al.* (1974) considered the development of andromonoecy a response to selection for increasing successful pollen transfer because vertebrates that are large relative to the stigma size have become the important pollinators. Ramirez *et al.* (1984) showed that *Bauhinia ungulata* [sub *B. benthamiana*], a bat and hummingbird-pollinated species, is also andromonoecious. They also showed that male flowers had short gynoecia and abortive ovules. They, like Heithaus *et al.*, favoured the hypothesis that andromonoecy is a mechanism to assure successful male gamete transfer and overcome the wastage incurred by large hovering pollinators. They considered resource limitations as a possible factor affecting sex expression, but dismissed this idea because there was no relationship between tree size and the proportion of male flowers. Bawa & Webb (1984) did not observe andromonoecy in the trees of *Bauhinia ungulata* in their study area in Costa Rica, but these authors did observe that fruit-set occurs mostly in

lower inflorescence positions in this species, and they commented that fruits initiated in the lower inflorescence may acquire maternal sink resources to the detriment of fruit initiation higher in the inflorescence.

Cruden and Hermann-Parker (1979) also explained andromonoecy in *C. pulcherrima* in terms of increasing pollen movement to conspecific stigmas. The butterfly-pollinated flowers of this species continually secreted nectar, with hermaphrodite flowers producing 3 to 4 times as much nectar as the smaller male flowers. The male flowers thus had less accessible nectar which necessitated more extensive probing by the butterflies, which consequently spent more time per male flower. This ensured repeated contact of the hovering insects wings with the anthers. In hermaphrodite flowers nectar reached higher levels in the flowers so that the butterflies hovered further from the corolla resulting in the removal of pollen by the stigma which was exserted beyond the stamens. Cruden and Hermann-Parker (1979) mentioned that flowers lower on an inflorescence tended to be hermaphrodite and those higher on the inflorescence male but they considered this arrangement a mechanism to increase outcrossing by encouraging the common bottom to top foraging pattern.

In *C. calycina* an average of only two (range 1—3) flowers are open per inflorescence per day, whereas in *C. pulcherrima* there are generally more. Pollinating bees that visit *C. calycina* flowers therefore move more often from inflorescence to inflorescence than do butterflies on *C. pulcherrima*. This might explain the apparently similar nectar yields found in male and hermaphrodite flowers of *C. calycina* which contrasts with Cruden and Hermann-Parker's (1979) findings for *C. pulcherrima*.

In some cases, andromonoecy can be facultative. Stephenson (1979) established that although flowers in the inflorescences of *Catalpa speciosa* (Bignoniaceae) are all initially potentially hermaphrodite, once three or so flowers had been successfully cross-pollinated, the next flowers to open were functionally male (stylar arms did not open to expose the stigma) whilst any flowers still in tight bud did not open and were resorbed.

There is no direct evidence of fruit-set controlling subsequent flower sexuality in the inflorescence of *C. calycina*, unlike the classic study of *Catalpa speciosa* by Stephenson (1979, 1980). However, the circumstantial evidence of negative correlation between fruit initiation in the lower third of the inflorescence and the occurrence of male flowers in the upper third, plus the fact that almost a quarter of infructescences sampled did have some

fruits in the upper thirds of the rhachis, does strongly suggest that there is no fixed quota of male flowers in the inflorescences of this species, but rather that floral sexuality, with a triggered flip to male flower production, is stimulated by fruiting success in the lower inflorescence. *C. calycina* and perhaps other caesalpinioid species such as *Bauhinia ungulata* merit further careful study in this respect.

Simpson and Neff (unpublished) have argued that since *Caesalpinia exilifolia* and *C. pumilio* are pollinated by bees,rather than large vertebrates or pollinators that hover, increased time-per-flower would not enhance pollen pickup and andromonoecy cannot be explained by the arguments used by Heithaus *et al.* (1974) and Cruden & Hermann-Parker (1979). They also proposed the alternative explanation that andromonoecy reflects resource limitation within inflorescences, with proximal flowers receiving sufficient nutrients for fruit maturation and distal flowers insufficient. This was supported by their findings that fruit set primarily on the lower parts of an inflorescence and that style length decreased with flower position up the rhachis so that upper flowers were functionally male. This pattern has been reported for *Solanum* by Symon (1979) and Whalen and Costick (1986). Simpson and Neff (unpublished) also predicted that if resource limitation is responsible for the pattern of andromonoecy found in the two *Caesalpinia* species then:

a) Distal flowers on an inflorescence are capable of maturing fruits, but the probability of this decreases with increasing fruit set lower on an inflorescence.

b) Andromonoecy should be best, or exclusively, expressed in large-fruited, out-crossing perennials and least well-expressed in self-pollinating, small-fruited annuals and/or weedy species.

In *Caesalpinia eriostachys*, the late blooming flowers in the upper one-third of the inflorescence generally function only as pollen donors, but if no fruits have been set in the lower part of the inflorescence then these flowers are more likely to set fruits(Bawa and Webb, 1984). This perfectly fits both of the above predictions of Simpson and Neff. My findings for *C. calycina* also fit this pattern.

3) **Fruit-set and seed-set**

Bawa et al. (1985) report from the work of Haber and Frankie (1982) that the lack of fruit set in several species following cross-pollinations may be attributed to three factors. First, it could be an artifact of hand-pollination techniques. Second, in most species, a

large number of flowers are aborted a day or two after anthesis and it is conceivable that some pollinations involved flowers destined to abort anyway. Third, if cross-pollinations involved close relatives, lack of fruit set could have resulted from inbreeding depression.

The low fruit set found in *C. calycina* (12%) is fairly typical of tropical trees (Bawa & Webb, 1984), and although lack of successful pollination has been proposed as an explanation for this phenomenon by some workers (e.g. Willson & Schemske, 1980; Bierzychudek, 1981), the continued loss of young fruits in the post-pollination period has led many workers to accept that limited availability of maternal resources puts an upper limit on fruit and seed development (Lloyd, 1980; Stephenson, 1981). Opinions differ as to what extent fruit/seed survival vs. rejection may be influenced by maternal filtration of genetic quality of developing embryos etc., or rather by more mechanical stimuli, e.g. first developing fruits gain the largest share of the resources.

Bawa and Webb (1984) found that for *C. eriostachys*, within an inflorescence, pods that were beginning to mature in the upper third were much more likely to be aborted than those in the lower or middle thirds. One possible reason for the loss of upper pods may be the cost involved in maturing more than one pod per inflorescence and the significantly greater investment in pedicel and peduncle thickening which is required to support upper rather than lower pods. Pedicel strength may be important in combatting the loss of fruits from high winds late in the dry season (Bawa & Webb, 1984). In *C. eriostachys* early blooming (lower) flowers set proportionately more fruits than late blooming ones, suggesting interference by older fruits in supply of resources to the younger ones. It is, however, also possible that once an optimal number of fruits has been set, more and more flowers are destined to fulfil only male function, (Bawa & Webb, 1984). In *C. calycina* a large proportion of the abscised flowers were functionally male.

Flower and juvenile fruit abscission permit plants to match fruit and seed number with the available resources over a wide range of environmental conditions (Stephenson, 1981). Bawa and Webb (1984) showed that in *C. eriostachys*, 93% of the flowers were aborted within 2 days, and of the young fruits present on day 3, 80% were also aborted. Fruit-set ranged from 0.50 to 1.41% among six trees. Within individual trees mature pods were not distributed at random among inflorescences. Inflorescences of *C. eriostachys* had, on average, 15-24 functional flowers and yet most inflorescences matured only a single pod. In a sample of 50 infructescences from each of 5 trees, 87.2% had only one pod, 12% had

2 and 0.8% had 3. Fruit set was consistently and significantly higher among early flowering branches than in midseason branches.

The pattern of seed abortion in *C. calycina* somewhat resembles that reported by Bawa & Buckley (1989) for other leguminous taxa, including caesalpinioids, with a decrease in seed abortion from a proximal to median positions, and then a further increase in abortion in the distal region. However, the 'steady state' abortion found in the first three seed positions in *C. calycina* (c. 24% at each) are rather different to the generalized "*Gliricidia*" pattern discussed by Bawa & Buckley (1989) in which a steady, or sometimes dramatic, decrease in seed abortion rate is shown from proximal to median positions. However, these authors were able to compare early vs. late seed abortion rates for these species.

In *C. eriostachys*, Bawa and Webb (1984) found that a variable number of seeds were set per pod and on average more than half of the ovules developed into good seeds. In the present study *C. pluviosa* var. *sanfranciscana* has sub-woody, pseudoseptate fruits very similar to those of *C. eriostachys*. Both have a greenish pithy mesocarp which completely separates each seed from its neighbour. In contrast, the mature fruit of *C. calycina* is an open-chambered leathery-valved pod. It seems probable that the different fruit types play a role in determining which ovules successfully set seed. The question of which ovules are more likely to set seed, and the difference between *C. calycina* and *C. pluviosa* var. *sanfranciscana*, may be influenced by the sequence in which ovules are penetrated by pollen tubes as they enter the ovary. All other factors being equal it is to be expected that basally located ovules (ie. those nearest the pedicel and thus the incoming food supply) to have a better survival chance but this is clearly not the case for either of the species in this study. Ovule abortion can also be seen to be non random in both taxa.

The nature of the late-acting SI present in *C. calycina* which may permit self-pollen tubes to 'usurp' ovules which might otherwise have been reached by a cross-pollen tube, may also contribute to some fruit/seed abortion. Waser & Price (1991) have shown that fecundity is reduced in this way in *Ipomopsis aggregata*.

Conclusions

The present study concentrated on *Caesalpinia calycina* which has inflorescences that open two flowers per day acropetaly. Upper flowers of an inflorescence can be

hermaphrodite with the potential to produce fruit or might be male due to suppression of pistil development. It appears that the switch to maleness is related to successful fruit set in lower flowers which thus restrict the resources available to upper flowers and/or fruits. The upper, functionally male flowers appear to produce a similar quantity of pollen and nectar to lower hermaphrodite flowers so that pollinators are equally attracted to both flower types and this increases the chance of cross-pollination by pollen transfer between plants. Most previous workers (e.g. Cruden & Hermann-Parker, 1979; Bullock, 1985) have stated or implied that for andromonoecious breeding systems the number of male flowers per inflorescence is fixed but the results of this study suggest that the switch to maleness, at least in *C. calycina*, is highly labile.

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